CERTAIN BASAL TELENCEPHALIC CENTERS IN THE CAT

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TWENTY-NINE FIGURES

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INTRODUCTION

The following study was undertaken to provide the necessary anatomic basis for experimental work on certain basal regions of the forebrain of the cat. Although there are several excellent accounts dealing with various forebrain regions and an atlas (Winkler and Potter, '14) which is of the greatest assistance in orientation, none of these provides the details of nuclear structure and fiber connections of the cat's telencephalon which are an essential background for the type of experimental work projected. Moreover, a description of the results is justified on the grounds that certain of the nuclear relations and fiber connections demonstrated in this study contribute to the present knowledge of mammalian forebrain anatomy and help to explain the general trend of development in this region.

To Prof. Elizabeth C. Crosby I am indebted for the opportunity of undertaking this problem. For her direction, constant help, and inspiration given me during the present study, I acknowledge my sincere appreciation.

MATERIAL AND METHODS

The cat brains used in the following study were cut serially in either transverse or sagittal planes and stained with toluidin blue (Huber, '27) to bring out the nuclear pattern, or prepared either by a medullary sheath stain or by one of the silver impregnation methods to demonstrate the medullated and unmedullated fiber systems. The toluidin blue material consists of a transverse and a sagittal series, both of which were prepared by the late Prof. G. Carl Huber. The fiber material includes one transverse series of adult cat brain stained by the Weil method (Weil, '28), one transverse series of the brain of a 2-day-old kitten stained by the modified Ranson pyridine silver method (Huber and Guild, '13), a similar series prepared by the Cajal method; and one transverse and one sagittal series of the brains of 3-week-old kittens stained by the Cajal method.

To facilitate the study of the tuberculum olfactorium—particularly to illustrate the arrangement of the granular islands of Calleja—a blotting paper model was constructed in the usual manner at a magnification of 39.4. The outer layers of the tuberculum olfactorium and the granular islands of Calleja were outlined at the above magnification on blotting paper and the cell groups were inked in on the paper. Then the tuberculum as outlined was cut out and the sheets of blotting paper were piled together in order, precautions being taken to maintain the proper axial and rostrocaudal relations.

GENERAL RÉSUMÉ OF THE LITERATURE

Specific references to the results of other observers are placed in the present paper with the descriptions to which they are pertinent. Here brief consideration will be given only to certain general contributions to the field of mammalian forebrain morphology and to reference books treating of this field. For an understanding of the anatomy of the cat's skull, and of the relations of the telencephalon to it, "The Anatomy of the Cat" by Reighard and Jennings ('25) is valuable; the Winkler and Potter Atlas ('14), dealing with certain major fiber systems and the nuclear pattern of the cat's brain, is very useful for establishing relations; and the Ariëns Kappers, Huber, and Crosby reference text ('36) provides a necessary background for the general field and is a source book for references to the special research papers. Elliot Smith's ('10) discussion of special problems related to the forebrain is of particular interest to investigators in this field. Among the special research contributions to the structure of various regions of the mammalian telencephalon may be mentioned the work of Livini ('08) on Hypsiprymnus, of Johnston ('23) on various mammals, of Obenchain ('25) on Caenolestes, of Sonntag and Woollard ('25) on Orycteropus, of Gurdjian ('25, '27, '28) on the rat, of Loo ('30, '31) on the opossum, of Young ('36) on the rabbit, of Humphrey ('36) on the bat, and of Crosby and Humphrey ('38, '39) on a wide range of submammalian and mammalian forms.

THE OLFACTORY AND ACCESSORY OLFACTORY BULBS WITH CONNECTIONS

General relations

The olfactory bulb, a rather prominent structure in the cat, appears almost kidney-shaped in gross material. It is so situated that its posterior, concavely-curved surface, corresponding roughly to the hilum of the kidney, is in contact dorsally with the frontal pole of the cortex and, more ventrally, is attached to the olfactory crus. Its ventral and anterior surfaces, lying against the cribriform plate of the ethmoid, form a continuous convex curve. Its dorsal surface, which, in keeping with the analogy, would correspond to the upper pole of the kidney, is more gently curved and almost flattened as it abuts the overlying frontal bone. The line of articulation of the bulb with the olfactory crus is the fissura circularis that separates these two structures and sharply outlines the more ventral part of the bulb's posterior, concave surface. The oblique direction of this fissure—which extends at nearly a 45° angle to the long axis of the brain—is such that the dorsal surface of the bulb is in a plane more anterior than its ventral caudal pole. Consequently cross sections may show an olfactory formation on one side of the section and a nuclear pattern typical of the crus on the other side.

On the dorsomedial surface of the olfactory bulb proper, as this bulb is narrowing down toward the crus, an eminence appears which receives the entering vomeronasal nerve. This eminence is spoken of as the accessory olfactory bulb or accessory olfactory formation (McCotter, '12; Herrick, '24; Young, '36; and others).

The olfactory formation

The olfactory formation of the carnivore has been frequently described and figured in investigations of the finer structure of the mammalian olfactory bulb, especially in Golgi studies (Golgi, 1875; Ramón y Cajal, 1890, '11; van Gehuchten and Martin, 1891; Blanes, 1898; Winkler and Potter, '14). The number of layers given for this formation has depended

on differences in classification and varies from three (Golgi) to eight (Winkler and Potter). The Ramón y Cajal terminology, employed in the present account, recognizes, beginning at the periphery (figs. 1, 3, 7): (1) a layer of entering nerve fibers; (2) a layer of glomeruli; (3) an external plexiform layer; (4) a layer of mitral cells; (5) a deep plexiform layer; (6) a layer of granule cells and white substance; and (7) an ependymal layer.

In the material studied, the superficial layer (the olfactory fila) is an intricate feltwork of non-medullated fibers, which covers all parts of the olfactory formation and thins out at more posterior levels. The fascicles are thickest at the summit and anterior end of the bulb and particularly in portions of the medial and lateral walls, thus indicating the path of distribution. They are thinnest along the surface below the frontal cortex (fig. 7) and it is from this surface that the olfactory formation first disappears. In the toluidin blue series this layer is outlined by neuroglia, but in the pyridine silver series a considerable number of fibers are darkly stained and can be traced into glomeruli.

The glomerular layer (figs. 1, 3, 7), although only a single glomerulus thick, is so disposed as to give a pseudostratified appearance in section. This layer is formed by the synaptic spheres between the incoming olfactory fibers and the mitral cells and includes the granule cells outlining these zones of synapse. These granule cells, which make up the external granular layer of some authors (Young, '36, and Humphrey, '36), are more numerous on the inner side of the glomeruli facing the external plexiform layer. The Golgi detail of these cells has been shown for the cat by Ramón y Cajal ('11; figs. 414, 416). They are mainly of the periglomerular type; however, toluidine blue preparations show an occasional intraglomerular cell.

The external plexiform layer (figs. 1, 3, 7) in cell preparation is a wide, clear area showing displaced mitral cells. In the pyridine silver series the main dendrites of some of the mitral cells can be seen crossing the layer to enter glomeruli.

ABBREVIATIONS

a, fibers entering the anterior commissure from the posterior part of the anterior olfactory nucleus and the anterior part of the tuberculum olfactorium
a.amyg.a., area amygdaloidea anterior
a.preopt., area preoptica
b, the portion of the central nucleus dorsal to the lateral amygdaloid nucleus
bulb.olf., bulbus olfactorius
bulb.olf.acc., bulbus olfactorius accessorius
c, fibers out of the lateral and basal nuclei cutting across the commissural component of the stria terminalis
c.fron., cortex frontalis
c.pyr., cortex pyriformis
cap.ext., capsula externa
cap.extr., capsula extrema
cap.int., capsula interna
ch.op., chiasma opticum
cing.g., gyrus cinguli
claus., claustrum
col.fx., columna fornicis
com.ant., commissura anterior
com.ant.l.ant., commissura anterior, anterior limb
com.ant.l.trans., commissura anterior, transverse limb
com.hip., commissura hippocampi
corp.cal., corpus callosum
cort., cortex
d, fibers from the lateral septal nucleus entering the nucleus accumbens
ext.a, external lamina of the pars lateralis of the anterior olfactory nucleus, dorsolateral to pars lateralis
ext.b, external lamina of the pars lateralis of the anterior olfactory nucleus, dorsal to pars lateralis
f.amy., fissure amygdaloidea
f.endorhin., fissura endorhinalis
f.rhin., fissura rhinalis
f.rhin.arc., fissura rhinalis arcuata
fil.olf., fila olfactoria
fim., fimbria
form.olf., formatio olfactoria
fx., fornix
fx.precom., fornix precommissuralis
fx.sup., fornix superior
genu corp.cal., genu corpus callosum
gl.pal., globus pallidus
hab., habenula
hip., hippocampus
hip.p.ant., hippocampus, pars anterior
hypothal., hypothalamus
ind.gr., indusium griseum
isl.Cal., island of Calleja
isl.cort., island cortex
isl.m.Cal., large medial island of Calleja
l.b., longitudinal association bundle
l.b.a., longitudinal association bundle, anterior division
l.b.p., longitudinal association bundle, posterior division
l.cel.mit., lamina cellularum (cellulae mitrales)
l.glom., lamina glomeruli
l.gran., lamina granularis
l.plex.ext., lamina plexiformis externa
l.plex.int., lamina plexiformis interna
M, large medial island of the tuberculum
m.f.b., medial forebrain bundle
m.interc., massa intercalata
N, an enclosed space in an island of the tuberculum
N.opt., nervus opticus
N.vomeronas., nervus vomeronasalis
n.acc., nucleus accumbens
n.ans.lent., nucleus ansae lenticularis
n.bas.amyg., nucleus basalis amygdalae
n.bas.amyg.p.lat., nucleus basalis amygdalae pars lateralis
n.bas.amyg.p.med., nucleus basalis amygdalae pars medialis
n.caud., nucleus caudatus

n.cent.amyg., nucleus centralis amygdalae
n.com.ant., nucleus commissurae anterioris
n.cort.amyg., nucleus corticalis amygdalae
n.d.b.B., nucleus of the diagonal band of Broca
n.entoped., nucleus entopeduncularis
n.gen.lat., nucleus geniculatus lateralis
n.interc.amyg., nucleus intercalatus amygdalae
n.interst.st.term., nucleus interstitialis striae terminalis
n.lat.amyg., nucleus lateralis amygdalae
n.med.amyg., nucleus medialis amygdalae
n.olf.ant.p.dor., nucleus olfactorius anterior pars dorsalis
n.olf.ant.p.ext., nucleus olfactorius anterior pars externa
n.olf.ant.p.lat., nucleus olfactorius anterior pars lateralis
n.olf.ant.p.med., nucleus olfactorius anterior pars medialis
n.olf.ant.p.post., nucleus olfactorius anterior pars posterior
n.olf.ant.p.vent., nucleus olfactorius anterior pars ventralis
n.sept.fimb., nucleus septo-fimbrialis
n.sept.lat., nucleus septalis lateralis
n.sept.med., nucleus septalis medialis
n.tr.olf.lat., nucleus tractus olfactorii lateralis
n.triang., nucleus triangularis
O and P, enclosed spaces in an island of the tuberculum
perivent.gr., periventricular gray
p.ped., pes pedunculi
put., putamen
s, stria terminalis fibers from the supracommissural component entering the septal region
s.s., stratum album superficiale
st.med., stria medullaris
st.L., stria Lancisii
st.term., stria terminalis
st.term.p.com., stria terminalis pars commissuralis
st.term.p.preop., stria terminalis pars preoptica
st.term.p.st.med., stria terminalis, stria medullaris portion
st.term.p.supracom., stria terminalis pars supracommissuralis
t, fibers from the tuberculum to the stria medullaris
tr.cort.sept., tractus cortico-septalis
tr.d.b.B., tract of diagonal band of Broca
tr.olf.interm., tractus olfactorius intermedius
tr.olf.lat., tractus olfactorius lateralis
tr.olf.lat.ped.dors., tractus olfactorius lateralis, pedunculus dorsalis
tr.olf.lat.ped.vent., tractus olfactorius lateralis, pedunculus ventralis
tr.olf.med.. tractus olfactorius medialis
tr.op., tractus opticus
tr.sept.cort., tractus septo-corticalis
tr.sept.hypothal., tractus septo-hypothalamicus
tub.olf., tuberculum olfactorium
tub.olf.l.plex., tuberculum olfactorium, lamina plexiformis
tub.olf.l.polym., tuberculum olfactorium, lamina polymorphia
tub.olf.l.pyram., tuberculum olfactorium, lamina pyramidalis
tub.olf.p.ext., tuberculum olfactorium pars externa
tub.olf.p.inter., tuberculum olfactorium pars intermedia
tub.olf.p.med., tuberculum olfactorium pars medialis
v.lat., ventriculus lateralis
v.olf., ventriculus olfactorius
v.III, ventriculus tertius
y, fibrous continuity between the globus pallidus and the diagonal band formation

Golgi studies indicate that this layer consists chiefly of radially running fibers, formed by dendritic branches and recurrent collaterals of the neuraxes of mitral cells, together with dendritic processes of granule cells.

The mitral cells (figs. 1, 2, 3), the largest neurons in the olfactory formation and also the demonstrated cells of origin for the olfactory tract, form a single row between the two plexiform layers. Their cell bodies are triangular, and about them are smaller cells, the 'cellules à houppette' of Ramón y Cajal ('11, fig. 423), which this author believed to give rise to the commissural fiber system of the olfactory bulb.

The internal plexiform layer (figs. 1, 3, 7) is very narrow. Although distinct in some parts of the sections, it is indistinct in other portions, and merges quickly with the layer of granule cells and with the white substance internal to it. The latter lamina, in transverse toluidin blue sections, shows deeply stained islands and lines of concentrically-placed granule cells, which leave room for the passage of fibers. On the inner side of the granule cells, near the ventricle, the Weil preparations show the medullated fibers which enter the olfactory tract.

Fig. 1 Transverse section through the olfactory bulb and the accessory olfactory bulb, showing the rostral end of the anterior olfactory nucleus and the two small external laminae, *a* and *b* associated with it. Toluidin blue preparation. × 9.

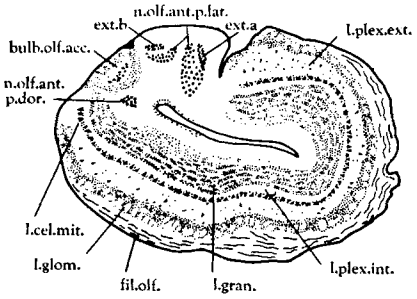
Fig. 2 Transverse section through the olfactory bulb and the accessory olfactory bulb, showing the entering vomeronasal nerve and the formation of the lateral and the intermediate olfactory tracts. Two-day-old kitten. Pyridine silver preparation. ×12.5.

Fig. 3 Transverse section through the olfactory bulb and crus, showing the horseshoe shape of the gray of the anterior olfactory nucleus. Toluidin blue preparation. × 9.

Fig. 4 Transverse section, slightly anterior to the tuberculum olfactorium, showing lateral, intermediate, and medial olfactory tracts. Two-day-old kitten. Pyridine silver preparation. × 9.

Fig. 5 Transverse section through the olfactory crus, showing the posterior extent of the pars externa of the anterior olfactory nucleus and the ring of gray about the ventricle. Toluidin blue preparation. × 9.

Fig. 6 Transverse section through the caudal end of the olfactory crus, showing the continuity of the frontal cortex and the pars dorsalis of the anterior olfactory nucleus. Toluidin blue preparation. × 9.



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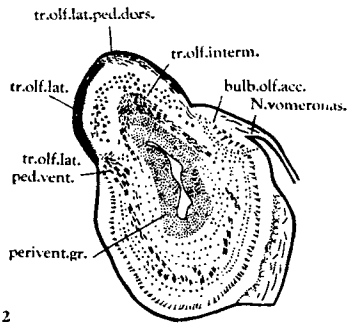

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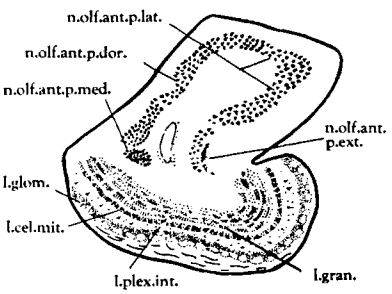

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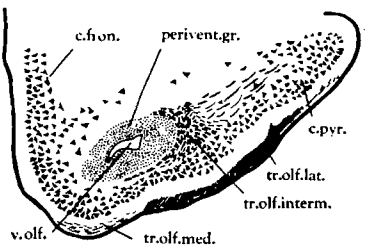

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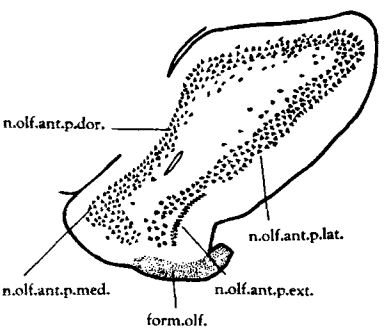

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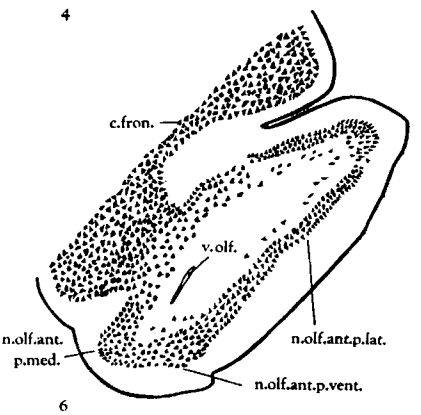

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Figures 1 to 6

In the transition from the bulbar formation to the olfactory crus, the olfactory formation first disappears dorsally; dorsomedially it is replaced by the accessory olfactory bulb (fig. 1). Gradually the olfactory formation recedes from the medial and lateral sides of the crus (fig. 3). The ventral tip of the olfactory formation continues farthest caudally (figs. 5, 7).

The ventricle of the bulb, a direct continuation of the lateral ventricle, is an elongated slit, mediolaterally compressed, and is larger here (fig. 1) than it is in the olfactory crus (figs. 3, 5).

The accessory olfactory formation

The accessory olfactory bulb has been described in many mammals and submammals and a summary of the literature pertinent to it can be found in the Ariëns Kappers, Huber, and Crosby text ('36) and in the recent paper by Crosby and Humphrey ('39). This structure is not always present in mammals. For example, it is not found in the bat (Humphrey, '36), is present only rarely in the macaque monkey (Crosby and Humphrey, '39), and apparently does not occur in adult man.

The accessory olfactory formation of the cat (figs. 1, 7) lies at the anterior end of the dorsomedial surface of the olfactory crus, immediately behind the olfactory formation and just ventral to the frontal cortex. In cross section it has the shape of a biconvex lens, with the greater convexity extending into the olfactory crus. It is approximately 2.5 mm. in length and appears cigar-shaped in sagittal sections. Its anteroposterior axis makes about a 30° angle with the base of the brain, placing its cephalic tip more dorsally than its caudal end.

In structure the accessory olfactory formation (figs. 1, 7) is similar to the olfactory formation. The superficial layer of nerve fibers is composed of the terminals of the vomeronasal nerve (fig. 2). McCotter ('12), by dissection methods, has followed this nerve to the accessory olfactory bulb in several mammals, including the cat, and Huber and Guild ('13) have traced it in sagittal pyridine silver series of the rabbit's whole head. The glomeruli in this region are smaller and the gran-

ule cells outlining them fewer in number than in the olfactory formation. A plexiform layer comparable to the external plexiform layer of the olfactory formation is interposed between the glomerular layer and the mitral cells, which are smaller and more irregularly placed than those of the olfactory formation. A granule cell layer, continuous with the homologous layer of the olfactory formation, makes up the

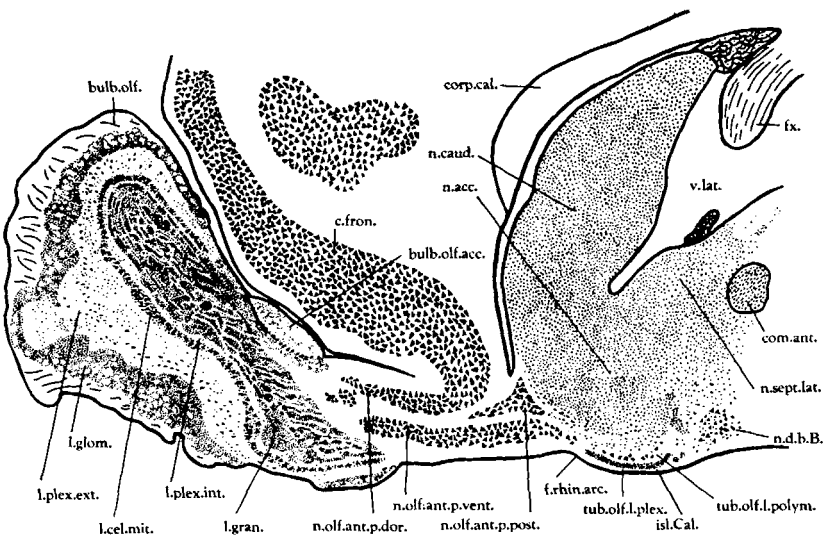


Fig. 7 Sagittal section through the accessory olfactory bulb showing the relations between the pars posterior of the anterior olfactory nucleus and the nucleus accumbens, and the pars ventralis of the anterior olfactory nucleus and the tuberculum olfactorium. Toluidin blue preparation. × 5.

innermost lamina of the accessory bulb, delimiting it in cross and sagittal sections. Gurdjian ('25) could not find this layer in the accessory olfactory bulb of the albino rat.

The fiber connections

The major incoming fascicles to the olfactory and accessory olfactory formations are the olfactory and the vomeronasal nerves respectively; the main outgoing connections are the olfactory tracts. The preparations available do not permit so

detailed a study of these systems as has been reported in certain forms, but lateral, medial and intermediate olfactory tracts are recognizable.

The lateral olfactory tract (figs. 2, 4, 14, 15) arises by two peduncles, dorsal and ventral, in essentially the same fashion as in the opossum (Herrick, '24) and in the rabbit (Young, '36). In transverse Weil preparations of the olfactory bulb, anterior to the accessory olfactory bulb, medullated fibers (not illustrated), passing dorsally along the medial and lateral sides of the ventricle, accumulate just dorsal to the more thinly myelinated fibers of the intermediate olfactory tract. The fibers on the medial and lateral sides of the ventricle are the respective forerunners of the dorsal and ventral peduncles. This becomes apparent when these fibers attain a superficial position on the dorsolateral aspect of the crus. From this region (fig. 2) caudalward the lateral olfactory tract grows as follows: The ventral peduncle feeds the ventral end of the lateral olfactory tract with fibers, first from the lateral side of the bulb, then from the ventral side of the bulb, and finally from the medial side of the bulb; the dorsal peduncle, carrying fibers from the accessory bulb, adds the same to the dorsal end of the lateral olfactory tract. Hence, in the fully formed lateral olfactory tract there is an orderly, dorsoventral arrangement of fibers from the olfactory and the accessory olfactory formations such that the most dorsal fibers are from the accessory olfactory portion and these are followed ventrally in succession by fibers from the anteromedial part of the bulb, from the anterolateral part of the bulb, from the posterolateral part of the bulb, and finally, most ventrally, by fibers from the posteromedial part of the bulb. In its course in the lateral portion of the crus, the lateral olfactory tract receives fibers from and contributes fibers to the pars lateralis of the anterior olfactory nucleus. Reaching the endorhinal fissure, it continues caudalward between the tuberculum olfactorium and the pyriform lobe and its fibers spread over the pyriform lobe cortex. Undoubtedly some of the tract distributes to certain of the amygdaloid nuclei—possibly also to the tuberculum

olfactorium—but the material available is not adequate to determine its ultimate distribution.

The intermediate olfactory tract (fig. 14) accumulates dorsal, then dorsolateral, and finally lateral to the ventricle. Its marked increase in size during its passage through the crus indicates not only that it is in functional relation with the olfactory formation but also that it has fibers to and from the nucleus olfactorius anterior, particularly from the pars dorsalis and the pars lateralis. Behind the crus this tract passes dorsolateral to the pars posterior of the anterior olfactory nucleus and dorsal to the anterior part of the tuberculum olfactorium. From both of these areas (a, fig. 14), and from the pyriform cortex, it receives fibers which together constitute a considerable component. The bundle, thus augmented, continues caudalward, receiving in course further fascicles from the pyriform lobe cortex, and then turns dorsomedially, under the head of the caudate nucleus, to enter the anterior commissure (figs. 15, 17, 18), of which it is the most rostral component.

The medial olfactory tract (fig. 4), which appears exceedingly small in the preparations available for study, lies in the ventromedial portion of the crus. It appears to enter into relation with the anterior continuation of the hippocampus and soon disappears from the field.

THE ANTERIOR OLFACTORY NUCLEUS

General relations

The olfactory crus (fig. 7) connects the olfactory bulb with the more specialized olfactory centers in the ventral part of the hemisphere. Its contained gray, the secondary olfactory gray in the path of the olfactory tracts, is the anterior olfactory nucleus. This nucleus has been described in the opossum by Herrick ('24), in Caenolestes by Obenchain ('25), in the albino rat by Gurdjian ('25), in Orycteropus by Sonntag and Woollard ('25), in the rabbit by Young ('36), in the bat by Humphrey ('36), and in a wide range of submammalian and mammalian forms by Crosby and Humphrey ('39). In homologizing this nucleus and its divisions in the cat with the com-

parable gray described in lower mammals it is necessary to consider the shape, position, and relations of the crus to structures immediately caudad to it and to the frontal cortex, since the outline of the nucleus follows the shape of the crus. For example, cross sections of the crus in the cat are trapezoid in shape (figs. 5, 6), whereas in the opossum (Herrick, '24, figs. 3, 4) similar sections are triangular to ovoid in outline. Furthermore, the crus is more obliquely placed in the cat so that the pars dorsalis of the anterior olfactory nucleus, which is continuous with the frontal cortex, is dorsomedial, although in the opossum it is dorsal in position.

The periventricular gray 'ring'

In the cross section series available the anterior olfactory nucleus is seen first in a plane slightly in front of the rostral tip of the accessory olfactory bulb, as a mass of cells dorsal to the ventricle. This is the dorsal part of the pars lateralis of the anterior olfactory nucleus. The more lateral portion of the pars lateralis appears in the dorsolateral part of the crus at the level of the rostral end of the granular layer of the accessory olfactory bulb (fig. 1). A little caudad the two unite into a single band, the pars lateralis of the anterior olfactory nucleus. Just behind this union, in sections through the posterior one-third of the accessory bulb, the pars dorsalis is seen in the dorsomedial part of the field, lateral to the accessory bulb. However, there is an interesting cell group, similar in position and in cell type to the pars dorsalis, which is present along the anterior one-third of the accessory bulb (fig. 1) but absent along its middle third. Apparently, this is the anterior end of the pars dorsalis cut off from the more caudal portion of the nucleus by fibers of passage.

Just caudad to the accessory olfactory bulb, in planes in which the olfactory formation still occupies the ventral part of the crus and the pars lateralis and the pars dorsalis form a horseshoe-shaped mass (fig. 3), the pars medialis of the anterior olfactory nucleus appears. Gradually the olfactory

formation disappears (fig. 5) and the pars ventralis (fig. 6) completes the ring of gray about the ventricle.

Followed caudalward, the pars lateralis of the anterior olfactory nucleus gradually fuses with the pyriform cortex (fig. 6) and the pars dorsalis grades over into the frontal cortex (figs. 6, 7). The anterior continuation of the hippocampus swings ventralward under the frontal cortex to come into relationship with the ventrally placed pars medialis of the nucleus olfactorius anterior (fig. 6), and the pars ventralis of the nucleus, continuing caudally, gradually fuses with the tuberculum olfactorium (fig. 7). Using the terminology here employed, the relations of the various parts of the nucleus olfactorius anterior with more caudally placed hemisphere centers agree very well with those described in the literature (Herrick, '24; Obenchain, '25; Humphrey, '36; Crosby and Humphrey, '39; and others). However, the pars lateralis, which is actually lateral and dorsolateral in the cat, and the pars dorsalis, which is dorsomedial in this carnivore, are proportionately very large, but the pars medialis, which lies ventromedially, is very small.

The pars externa

In the various mammals in which the anterior olfactory nucleus has been studied there is a tendency for a thin lamina of deeper staining cells to be drawn out peripherally from the nucleus olfactorius anterior, apparently under neurobiotactic influences related to the formation of the olfactory tract (Obenchain, '25; Young, '36). The cat has several small laminae of this nature peculiar to itself and one larger lamina in particular which is similar to that described in other mammals. This larger lamina is a sheet of deeply staining cells lying along the lower lateral part of the pars lateralis (figs. 3, 5), from which it is separated by a light plexiform layer. This pars externa of the anterior olfactory nucleus (Herrick, '24) stands out in both sagittal and cross sections. Beginning in a plane through the middle of the accessory olfactory bulb, it continues caudalward (fig. 3) in a position dorsal and poste-

rior to the receding granular layer of the olfactory formation, ending a few sections caudal to this layer (fig. 3). It lies thus in the path of the ventral peduncle of the lateral olfactory tract and is best developed in planes in which this peduncle is most prominent. In the opossum (Herrick, '24), in Caenolestes (Obenchain, '25), and in the rabbit (Young, '36) there is a dorsal limb to the pars externa. In the cat there is a lamina of cells along the dorsolateral side of the pars lateralis (fig. 1, ext.a) that begins at its anterior end and fuses with the pars lateralis before the more ventrally lying part of the pars externa, mentioned above, puts in its appearance. Further, there is a sheet of cells (fig. 1, ext.b) drawn off from the rostral end of the dorsal part of the pars lateralis of the anterior olfactory nucleus which fuses with the pars lateralis at the caudal level of the anterior one-third of the accessory bulb and then reappears as a separate mass a few sections farther on. It continues to a level just beyond the caudal limits of this accessory formation. Sagittal sections through the dorsal part of the pars lateralis show that the main mass of this pars lateralis is wavy in appearance and that the above-mentioned lamina of cells stretches between the crests of three contiguous waves. The pars externa a and the pars externa b have the same relation to the dorsal peduncle of the olfactory tract as has the pars externa to the ventral peduncle.

The pars posterior

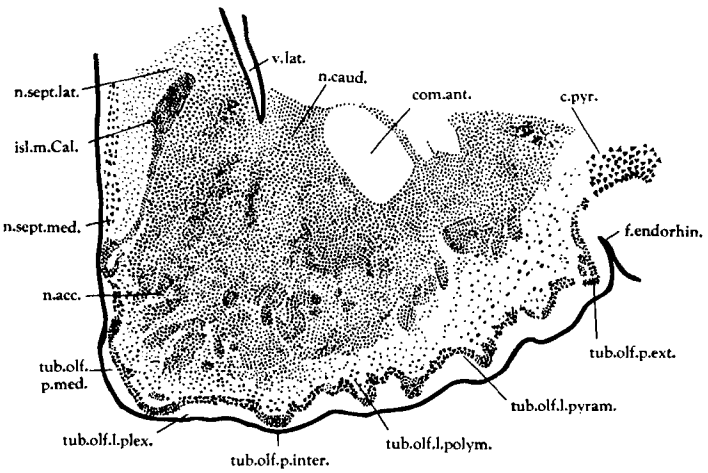
Near the region in which the ventricle of the crus becomes continuous with the lateral ventricle, a pyramidal mass of cells appears which constitutes the pars posterior of the anterior olfactory nucleus. This gray is similar in position to the homologous cell mass described in Caenolestes by Obenchain ('25). It extends caudalward above the posterior part of the pars ventralis and disappears at the anteroventral end of the caudate nucleus. This relation is particularly clear in sagittal sections, which show the pars posterior concavely curved to fit the contour of the head of the caudate nucleus but separated from this nucleus by a plexiform layer (fig. 7).

The nucleus olfactorius anterior both gives and receives fibers from the olfactory system (see p. 12). In addition to these secondary olfactory fibers, certain special connections of this nucleus, although small, can be recognized, among which are olfacto-frontal and olfacto-hippocampal fascicles. Such fibers are of fine internuclear type, not arranged in definite tracts but consisting of small bundles connecting the pars dorsalis of the nucleus olfactorius anterior with the frontal cortex on the one hand and the pars medialis of the anterior olfactory nucleus with the anterior continuation of the hippocampus on the other hand. These latter accompany the poorly developed medial olfactory tract. They are too fine to be shown clearly at the scale of the drawing but they occur at the level of figure 4.

THE TUBERCULUM OLFACTORIUM

General relations

The tuberculum olfactorium (figs. 7, 8, 9, 10a and 10b) lies immediately behind the pars ventralis of the anterior olfactory nucleus and is bounded laterally by the pyriform lobe. Posteriorly, it is directly continuous with the diagonal band of Broca (figs. 7, 9) and, medially, it projects into the basal region of the medial wall of the hemisphere, to come into relationship, successively, with the frontal cortex, the anterior continuation of the hippocampus (fig. 11), the lateral septal nucleus, the large-celled portion of the medial septal nucleus (figs. 8, 12), and the diagonal band of Broca (figs. 9, 13). Completely surrounded by the fissure rhinalis arcuata or sulcus arcuatus of Retzius (1898), the tuberculum is narrower anteriorly than posteriorly, and forms, as it does in a number of mammals (see Beccari, '10, figs. 1–16, especially fig. 8 of the dog), a prominent lobulated projection on the ventral surface of the brain. The furrows responsible for this lobulation, seen grossly, are for the most part directed anteroposteriorly. Further, they influence the corrugated appearance of the 'cortex' of the tuberculum olfactorium, an effect in keeping with their direction, since this corrugation is striking in cross sections but scarcely apparent in sagittal sections.



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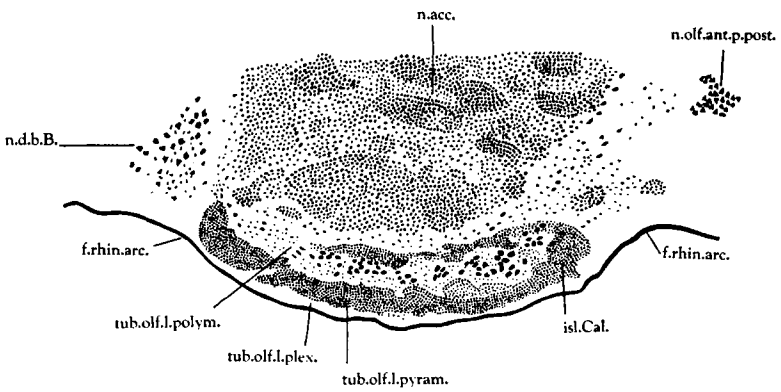

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Fig. 8 Transverse section through the tuberculum olfactorium, cutting the large medial island of Calleja. Toluidin blue preparation. × 10.

Fig. 9 Sagittal section of the tuberculum olfactorium cutting the point P, shown in figures 10a and 10b. Notice the large efferent cells in the enclosed sausage-shaped space. × 25.

Nuclear structure

The finer histology of the tuberculum has been studied by Calleja (1893), Beccari ('10) and Ramón y Cajal ('11), and three layers have been described—a plexiform layer, a pyramidal layer, and a polymorph layer. These layers are easily recognized in the cell preparations of the cat brain, though the limits of the plexiform and polymorph layers are not distinct in every region. The polymorph layer (figs. 7, 8, 9) has medium-sized pyramidal cells, fusiform cells, and a large efferent type of neuron to which Obenchain ('25) has called particular attention. Moreover, it is this layer that is continuous rostrally with the pars ventralis of the anterior olfactory nucleus and posteriorly with the nucleus of the diagonal band of Broca, a relationship easily seen in sagittal sections (fig. 9). The pyramidal layer (fig. 8) is an undulating sheet of closely packed, small and medium-sized pyramidal cells and contains varying quantities of granule cells.

Outstandingly characteristic of the tuberculum are the islands of Calleja (figs. 7, 8, 9), which have been divided into types (Beccari, '10) on the basis of their position and composition. Three kinds of islands were recognized by Loo ('31) in the opossum: (1) islands of granule cells; (2) islands of medium-sized pyramidal cells; (3) islands of small-sized pyramidal cells. In the cat the predominating type is the granular island, and the other islands, few and insignificant, are confined to the deeper part of the polymorph layer. In a few instances there appear to be pyramidal islands in the plexiform layer, but on following the sections they prove to be jutting edges of the pyramidal layer projecting into the plexiform layer. Serial cross sections indicate that a single large granular island extends into all three layers of the tuberculum. Usually such an island is embedded in the pyramidal layer and helps to produce its corrugated appearance. However, at certain points, it breaks through to the plexiform layer and may actually eliminate it. At still other points the pyramidal layer, although bent down by a granular island,

remains complete and restrains the island within the polymorph layer.

In the course of the present work a blotting paper model (figs. 10a, 10b) was made of the granular islands, showing the size and irregular contours of these highly interesting structures. In general the islands are larger in the caudal than in the rostral part of the tuberculum, and the largest islands are located medially and the smallest laterally. Their greatest dimension is in the anteroposterior direction, save for the largest island of all (fig. 8 and M of figs. 10a, 10b), which ascends most dorsally into the septal region and which has its greatest dimension dorsoventrally.

One thing which the reconstruction does not show, but which was evident in its preparation, is the tubular to spherical spaces enclosed by certain parts of these masses of granule cells. For example, at both the points 'N' and 'O' in the model (figs. 10a, 10b) there are spherically enclosed spaces and, at the point 'P,' there is a sausage-shaped space. It seems probable that these are the structures figured in cross section by Beccari ('10, fig. 23, Talpa, "nidi del Calleja ad anello"). Such spaces and cup-shaped depressions in other granular islands contain large efferent cells of the type found in the polymorph layer. Figure 9, taken from a series other than that from which the model was made, shows a sagittal section through the tuberculum at approximately the point 'P.' Here are seen the large efferent type of cells in the sausage-shaped space referred to above.

In the opossum (Loo, '31), the rabbit (Young, '36), and certain other mammals, three regions—medial, intermediate, and lateral—can be recognized in the tuberculum. Although there is no sharp line of separation between them, these areas are distinguishable in the cat and useful for descriptive purposes. The pars medialis (fig. 8) is that portion of the tuberculum which invades the medial hemisphere wall. Its cephalo-caudal extent is not so great as that of the pars intermedia and the three layers characteristic of the tuberculum can be seen only in its ventral part. Both the plexiform and the polymorph

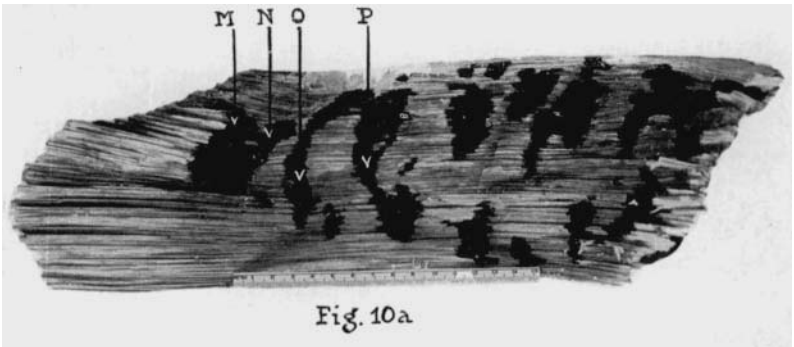


Fig. 10a Photograph of the blotting paper model of the islands of Calleja. Viewed from above. The metric scale is shown in the anterior part of the field. M is the large medial island. N, O, and P indicate the positions of enclosed spaces. × 6.5.

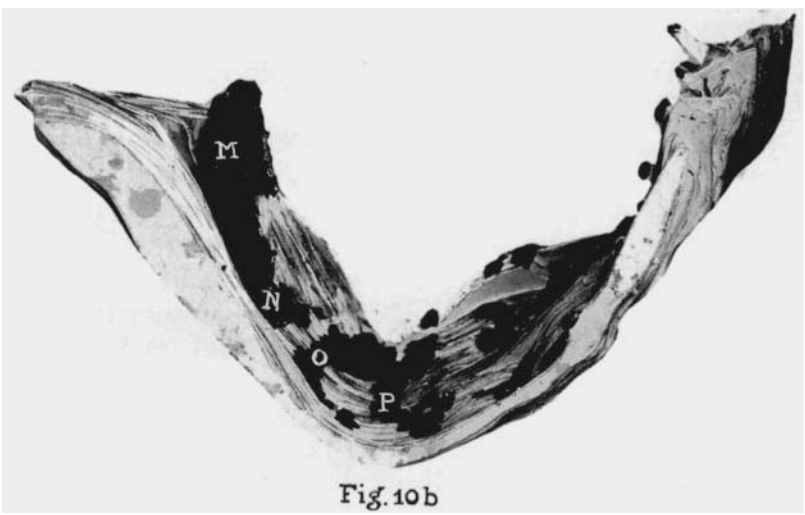


Fig. 10b Photograph of the blotting paper model. Anterior view. Legends the same as in figure 10a. × 6.5.

layers are greatly reduced, and, in the pyramidal layer, the proportion of pyramidal cells is small due to the size of the granular islands. Dorsally is the large granular island which contacts the lateral septal nucleus laterally and the nucleus accumbens medially, thus eliminating the plexiform and polymorph layers. The pars intermedia is the most extensive division of the tuberculum and includes most of its exposed surface (fig. 8). Here lies the transitional zone between the anterior olfactory nucleus and the polymorph layer of the tuberculum. Further, throughout the greater part of its extent, the dorsal limit of the polymorph layer is not sharply separable from the head of the caudate and the term 'striotubercular fusion' employed by Obenchain ('25) is an apt one. All three layers are present. The granular islands are of good size and are larger in the caudal than in the anterior part of the field. The pars lateralis (fig. 8, tub.olf.p.ext.), which is relatively small, parallels the pyriform cortex and lies below the anterior end of the putamen. All the layers are well developed. The pyramidal layer contains more pyramidal cells than it does in the other divisions of the tuberculum, and, as a corollary of this, the granular islands are smaller. The polymorph layer is wide and extends to the overlying putamen.

The foregoing description is based on a mediolateral division of the tuberculum olfactorium. In the Ramón y Cajal text ('11, p. 728, fig. 465), a figure drawn in the sagittal plane and a description of this region in the cat may be found. To this area Ramón y Cajal allocated everything from the base of the crus through the preoptic area. The tuberculum olfactorium of the present account includes roughly the anterior two-thirds of this area; that is, Ramón y Cajal's anterior and intermediate subdivisions. The plane of his section obviously, for the most part, cuts between the granular islands rostrally. In the bat (Humphrey, '36), the anterior part of the tuberculum is much less well developed and only the caudal portion, corresponding to Ramón y Cajal's intermediate division, shows medial, intermediate, and lateral subdivisions.

The fiber connections

The tuberculum olfactorium has been said by many observers (Elliot Smith, '09; Obenchain, '25; Gurdjian, '25; Loo, '31; and others) to receive olfactory fibers. Elliot Smith regarded its size as directly related to that of the olfactory system. Beccari ('10), however, believed such olfactory fibers to be confined to the more rostral portion of the tuberculum olfactorium, and earlier Ramón y Cajal ('01) was unable to demonstrate olfactory fibers to this region in Marchi preparations. His material of necessity would not show the unmedullated terminals. The number of olfactory fibers demonstrable in the cat material studied is very small and such fascicles are confined to the lateral border of the tuberculum. Dorsoventrally running tuberculo-septal and septo-tubercular bundles, of the type generally described for mammals (see Ariëns Kappers, Huber and Crosby, '36), are easily recognizable. Fibers, in part at least of cortico-tubercular type, run through the septal area with the precommissural portions of the fornix (fig. 18) to reach the tuberculum. The medial forebrain bundle (figs. 15, 17) receives fascicles from this area which interconnect the tuberculum and the hypothalamus. The relations to the diagonal band will be considered under the description of the septum (p. 35). The Weil preparations show a considerable number of fibers emerging from the concavities of the islands of the tuberculum and passing in a dorsocaudal direction. Due to the plane of section of this particular series they are easily followed. They converge lateral to the nucleus of the stria terminalis (fig. 15, t) and from this point can be traced dorsally to the stria medullaris. Presumably they pass to the habenula.

THE SEPTAL AREAS

General relations

The term septum has a special connotation in comparative neurology, for it designates that basal area lying beneath the corpus callosum in the anteromedial wall of the hemisphere,

extending laterally as far as the lateral ventricle, anteroposteriorly from the frontal cortex to the gray of the hippocampal commissure, and ventrally to the underlying tuberculum olfactorium and the preoptic area. A portion of this area is rostral to the anterior commissure (the precommissural septum) and a part is dorsal and caudal to this commissure (the postcommissural septum). From the postcommissural septum is developed the septum pellucidum of human anatomy, which area in man still contains septal gray in spite of its thinness. Other names have been used in the description of the whole or parts of this area, such as the corpus precommissurale (Elliot Smith, 1896, 1897), the corpus paraterminale (Elliot Smith, '03), and the paraolfactory area (Johnston, '13), but the question of terminology has been frequently discussed in the literature (Johnston, '23; Herrick, '24; Loo, '31; Ariëns Kappers, Huber and Crosby, '36), and there is no necessity for entering into it here.

On the basis of cell continuity and of fiber connections (pp. 28 and 37), and most particularly because of the relationship existing between the ventromedial quadrant of the hemisphere and the basal or striatal portion of the lateral hemisphere wall, the gray of the septum is grouped into two lines, a medial and a lateral. The medial line of septal gray will be considered first.

The medial line of septal gray

From the nucleus olfactorius anterior to the nucleus triangularis, a continuous line of gray can be traced from the olfactory bulb to a position on the upper surface of the anterior commissure. This stretch, in the septal part of its course, occupies the most medial portion of the septal area and consists of the anterior continuation of the hippocampus, the medial septal nucleus, and the nucleus of the diagonal band (interspersed in the posterior part of the medial septal nucleus), the bed nucleus of the anterior commissure, the nucleus triangularis, and the nucleus septo-hippocampalis, if present.

Further, this anteroposterior midline gray has, in the nucleus known as the diagonal band, a mediolateral extension which forms a bridge of gray between the septal regions and the basal area of the lateral hemisphere wall.

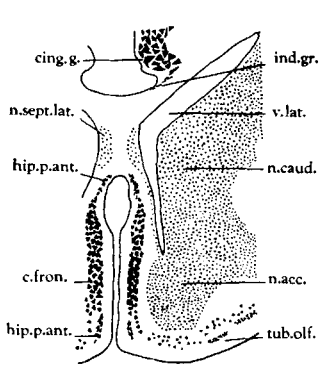
The anterior continuation of the hippocampus. This structure, present in such acallosal mammals as the opossum (Gray, '24; Loo, '31) and Caenolestes (Obenchain, '25) and likewise described in such callosal mammals as the rat (Gurdjian, '25), Orycteropus (Sonntag and Woollard, '25), the rabbit (Young, '36), and the bat (Humphrey, '36), is found in the cat. The anterior continuation of the hippocampus, which is a forward extension of the indusium griseum, enters the septal area after passing over the genu of the corpus callosum. However, through this area it does not show the steep descent which characterizes its course in the rabbit (Young, '36, fig. 17) but rather forms a double curve, first turning caudalward and then ventralward beneath the corpus callosum and behind the frontal cortex, which presses on it anteriorly. Figure 11 shows the anterior continuation of the hippocampus both above and below the frontal cortex. In the ventral part of its extent this anterior continuation passes rostrally beneath the frontal cortex to reach the pars medialis of the anterior olfactory nucleus. Its cells are of the small, pyramidal variety and appear as a deep staining band through the anterior part of the septal region.

Nucleus septo-hippocampalis. This nucleus, described by Young ('36) for the rabbit and by Humphrey ('36) for the bat, could not be found in the toluidin blue material available, but vestiges of it are present in two of the silver series used in the present study and, in each instance, it shows a different degree of development. This is interesting in the light of its phylogenetic and ontogenetic history, since this nucleus is the equivalent of the primordium hippocampi of the turtle (Johnston, '15) and of the alligator (Crosby, '17) and is related to a corresponding structure of the human embryo (Hines, '23; see Ariëns Kappers, Huber and Crosby, '36). In the pyridine silver series of the 2-day kitten, it can be clearly identified as

a small mass of deep staining cells on only one side of the septum and extending from the anterior continuation of the hippocampus to the nucleus triangularis. In the Cajal series of the 2-day-old kitten, it is on each side of the septal area, but it extends for only a few sections posterior to the anterior continuation of the hippocampus, with which it is continuous. Nucleus septalis dorsalis (Loo, '31) of the opossum is representative of the septo-hippocampal complex in this marsupial.

Nucleus medialis septi. This nucleus, lying immediately behind the anterior continuation of the hippocampus, occupies at first the free edge of the septal area along the ventral fissure. With the gradual recession of this fissure, it lies just lateral to the raphé, in which position it continues to the anterior commissure and its bed nucleus. Anteroventrally it contacts the tuberculum olfactorium, particularly the latter's polymorph layer. Posteroventrally, just behind the septal portion of the tuberculum, it comes into relationship with the nucleus of the diagonal band of Broca. In the cat the medial septal nucleus has, as Loo ('31) has shown for the opossum, a small-celled anterior portion and a large-celled posterior portion (fig. 12). The transition between these two divisions is gradual. The small-celled anterior portion is intimately associated with the anterior continuation of the hippocampus and the large-celled posterior portion is similarly associated with the nucleus of the diagonal band of Broca. In this latter instance the cells of these two nuclei are similar, and a line of separation between the large-celled portion of the medial septal nucleus and the nucleus of the diagonal band is arbitrary. Just rostral to the anterior commissure, some of the cells at the caudal end of the medial septal nucleus of each side invade the raphé (fig. 13) and form the 'commissure protoplasmique' of Ramón y Cajal ('11).

Nucleus septalis triangularis (fig. 13). This nucleus, named by Ramón y Cajal ('11) and studied more recently by Loo ('31) and Young ('36), is regarded as a condensation of the bed nucleus of the hippocampal commissure. In the toluidin



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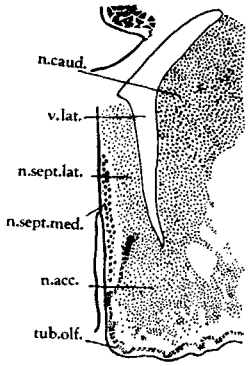

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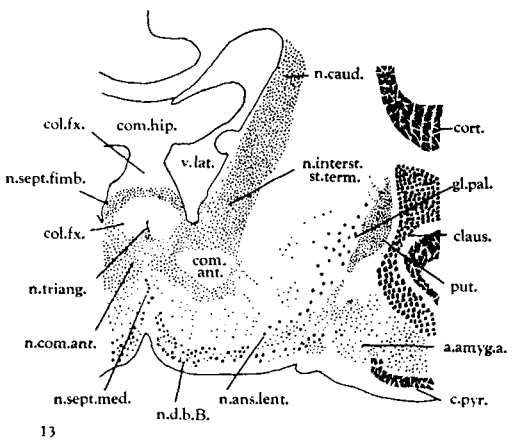

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Fig. 11 Transverse section showing the anterior continuation of the hippocampus both above and below the frontal cortex; also the anterior end of the lateral septal nucleus. Toluidin blue preparation. × 4.

Fig. 12 Transverse section through the middle of the septum, showing the lateral septal nucleus and the large-celled part of the medial septal nucleus. Toluidin blue preparation. × 4.

Fig. 13 Transverse section just anterior to the anterior commissure, indicating the various extensions of the nucleus of the diagonal band of Broca and its relation to the medial septal nucleus. Toluidin blue preparation. × 4.

blue transverse series it appears as a small but conspicuous triangular mass of deeply staining cells wedged in between the two descending columns of the fornix on the dorsal surface of the anterior commissure. From the apex of this nuclear mass, a few cells stream dorsally into the nucleus septofimbrialis.

Nucleus of the diagonal band of Broca (fig. 13). Although only a small part of this nucleus is in the septum it is considered here because of the relationship existing between it and the medial septal nucleus (Johnston, '23; Loo, '31; Young, '36; Humphrey, '36). Moreover, as was mentioned above, it forms a lateral extension of the medial line of septal gray that passes to certain basal centers in the lateral hemisphere wall. It consists of oval and irregular, medium-sized cells, together with a considerable quantity of large cells, not unlike the large cells of the medial septal nucleus, and, as Johnston ('23) has pointed out, comparable to the large cells of the globus pallidus. In the toluidin blue transverse sections, the aggregation of these cells makes a deep staining band which curves down from the septum (fig. 13) to reach the basal surface of the brain and then sweeps laterally across the posterior aspect of the polymorph layer of the tuberculum olfactorium and the anterior part of the preoptic area. In its course from the septum, it passes ventral to and through the medial forebrain bundle, in which some of its cells make up the nucleus preopticus magnocellularis; then, continuing lateralward, it splits into a dorsal and a ventral stream. The ventral part of the cellular stream flows into the anterior amygdaloid area, a relationship of the diagonal band emphasized by Johnston ('15 and '23) and noted by Loo ('31), Young ('36), and Humphrey ('36). In the cat, the dorsal part of the stream flows into an anteroventral extension from the globus pallidus sometimes termed the nucleus ansae lenticularis (Winkler and Potter, '14, plate VII). This cellular continuity of the diagonal band with the globus pallidus was observed by Young ('36) in the rabbit.

The lateral line of septal gray

A lateral line of gray, comparable in general to the medial band just described, can be traced through the septal area. This lateral band, which is formed by the nucleus accumbens, the lateral septal nucleus, the nucleus septo-fimbrialis, and the bed nuclei of the stria terminalis and of the anterior commissure, extends continuously from the transitional region between the anterior olfactory nucleus and the tuberculum olfactorium to the gray of the hippocampal commissure.

Nucleus accumbens septi (figs. 8, 11, 12). This nucleus, strictly speaking, is a medial, subventricular continuation of the striatum, but is considered here because of its relationship to the septal area. It is the most anteromedial portion of the caudate nucleus and includes that portion of the striatum which is medial to the sagittal plane passing through the ventral tip of the anterior horn of the lateral ventricle. In the rabbit, Young ('36) extended this plane as far laterally as the interbulbar component of the anterior commissure. Anteriorly the nucleus accumbens approaches the anterior olfactory nucleus. Its relation to the pars posterior of this nucleus has been given previously (p. 16, fig. 7). In the regions in which its convex-medial and ventromedial surfaces overlie the polymorph layer of the tuberculum, it presents the jagged appearance of the strio-tubercular fusion, and even the cellular arrangement of its deeper part is patchy, due to the passage of fibers (compare figs. 8, 12 with fig. 11). Dorsomedially neurons of the nucleus accumbens septi are continuous with the cells of the lateral septal nucleus and the large medial island of the tuberculum (fig. 8). Posteriorly the nucleus accumbens is confluent with the bed nuclei of the anterior commissure and the stria terminalis (fig. 13).

Nucleus lateralis septi. The lateral septal nucleus, the largest nuclear mass in the septum, occupies the septal area bordering the medial wall of the lateral ventricle. Its dorsoventral, mediolateral, and anteroposterior dimensions exceed those of the medial septal nucleus. Anteriorly it appears

dorsolateral to the anterior continuation of the hippocampus, before the medial septal nucleus has put in its appearance (fig. 11). Anteroventrally it is continuous with the transitional gray between the anterior olfactory nucleus and the tuberculum olfactorium. In the rostral part of their extent the lateral septal nuclei of the two sides (each resting on its respective nucleus accumbens) make an arch of gray along the sides and over the top of the two medial septal nuclei. Only a narrow, mid-dorsal, cell-free zone for the passage of precommissural fornix fibers prevents the completion of this gray arch dorsally (fig. 12). The large medial island of the tuberculum is interposed between the lateral septal nucleus and the nucleus accumbens, but in places these latter two nuclei, which have cells of similar type, blend intimately with each other. Caudalward the lateral septal nucleus is gradually pushed lateralward by precommissural and then by postcommissural fornix fibers. At the level of the anterior commissure the nucleus, greatly reduced, passes over into the bed nuclei of the anterior commissure and the stria terminalis. A few cells extend dorsally above the anterior commissure to become continuous with the nucleus septalis fimbrialis. In the cat there is no evidence for a division of the lateral septal nucleus into the dorsal and ventral parts found by Loo ('31) in the opossum.

Ramón y Cajal ('11) has figured Golgi preparations of the cells of the lateral septal nucleus in the rabbit and in the mouse. These cells have short, spiny dendrites and thin, descending neuraxes. He says ('11, p. 786), "Leur corps, de dimensions moyennes, est comparable à celui des neurons dominants du corps strié."

Nucleus septalis fimbrialis (fig. 13). This cell mass, a caudal continuation of the lateral septal nucleus, lies along the lateral side of the descending columns of the fornix and, as the fornix columns turn caudad above the anterior commissure, extends dorsally over these columns to meet its fellow of the opposite side. Loo ('31) found that it contributed fibers to the septohabenular path in the opossum and, on this basis, separated

it from the lateral, septal nucleus. Young ('36) made the same observation in the rabbit. In the three transverse silver series used in the present study, there is a dense feltwork of fine, unmedullated fibers at the side of the fornix columns in the position of this nucleus, from which fibers can be clearly followed to the stria medullaris.

Bed nuclei of the anterior commissure and of the stria terminalis (fig. 13). These two nuclei, composed of the same types of neurons, are inseparable in cell preparations and so are considered together. The rostral and ventral sides of the anterior commissure are faced with cells which extend to the underlying preoptic area and which are in contact with the nucleus triangularis (p. 28), the medial septal nucleus (p. 26), the lateral septal nucleus (p. 30), the nucleus septalis fimbrialis (p. 30), and the nucleus accumbens (p. 29). Furthermore, a considerable part of the cells in front of the anterior commissure form a bed nucleus for the supracommissural component of the stria terminalis, which, in the cat, is the largest part of this stria.

Dorsal to the anterior commissure, along the lower, lateral side of the lateral ventricle (fig. 13) and below the caudate nucleus, are neurons lying in the path of the strial fibers as these fibers descend to come into their various relations with the anterior commissure. The strial bed in the cat does not follow the stria terminalis in its course from the anterior commissure to the temporal region but disappears as the anterior thalamic nuclei are reached, a relationship which differs from that found in the opossum (Johnston, '23 and Loo, '31) but which is similar to that seen in the rat (Gurdjian, '27) and in the rabbit (Young, '36).

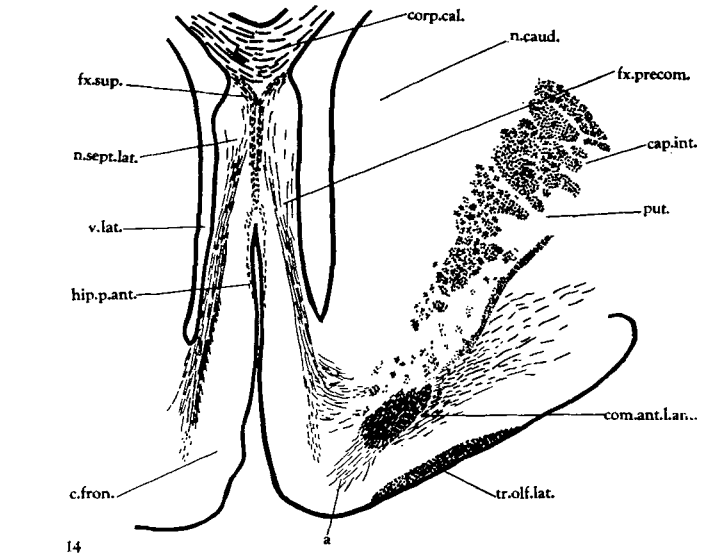
The fiber connections

The septum is a subcortical way station in the path of fornix fibers, its medial and lateral nuclei being particularly related to the precommissural fornix and its nucleus septalis fimbrialis being associated in similar fashion with the postcommissural fornix. These divisions of the fornix system, precom-

missural and postcommissural, have been described for the mammalian forebrain under various names by many observers (von Kölliker, 1894, 1896; Elliot Smith, 1896, 1896 a, 1897 a, 1897 b, '10; Loo, '31; Young, '36; Humphrey, '36; and others). In callosal mammals, the precommissural fibers (see fig. 621, Ariëns Kappers, Huber and Crosby, '36) reach the septum by various pathways which course in relation to the corpus callosum and the hippocampal commissure.

All these paths are well represented in the cat. The most dorsal fibers, the stria Lancisii, pass over the genu of the corpus callosum and enter the cephalic portion of the septum with the anterior continuation of the hippocampus.

Descending through the small-celled portion of the medial septal nucleus, some of its fascicles follow the anterior continuation of the hippocampus (fig. 14, hip.p.ant.), perhaps constituting the fasciculus marginalis of Elliot Smith (1897 a), and others swing out laterally and become associated with fibers of the lateral septal nucleus. The largest division of the precommissural fornix system (figs. 14, 16, 17), the fornix superior of von Kölliker, appears posteriorly on each side of the midline between the hippocampal commissure and the overlying corpus callosum. Incorporated in it are many 'fibrae perforantes,' which, in the silver series available, are seen passing through the corpus callosum at irregular intervals. Enroute through the dorsal part of the septum, the fornix superior gives off fibers to the medial septal nucleus and the medial side of the lateral septal nucleus. Its most anterior fibers can be traced as far forward as the genu of the corpus callosum, in which region they descend in front of the nucleus accumbens. A large proportion of them, however, turn sharply caudad and, passing ventrolaterally, proceed to the medial wall of the lateral ventricle to distribute to the lateral septal nucleus. The interesting curved course of these latter fibers can be followed only in the Cajal series of the 3-week-old kitten. Unmyelinated, they are well impregnated in this series, and form a deep staining sheet of fibers adjacent to the ventricle in the lateral part of the septum (fig. 16).



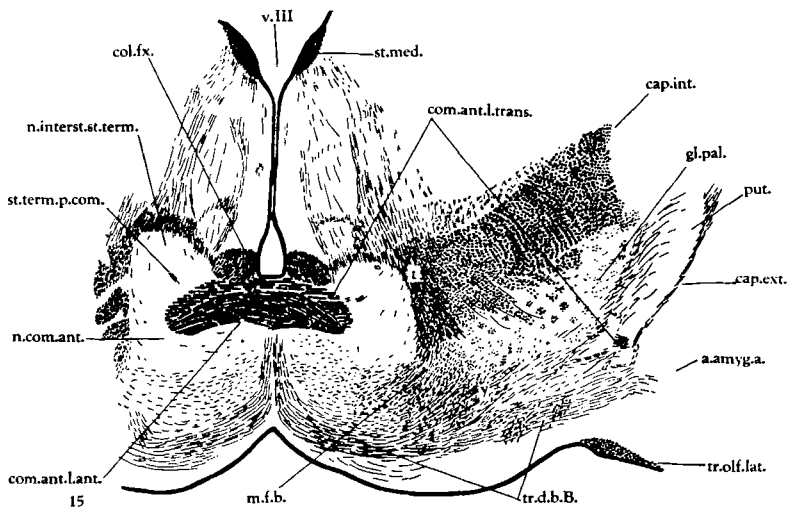


Fig. 14 Transverse section through the most cephalic part of the septum to show the fibers associated with the anterior continuation of the hippocampus. This series is somewhat tilted. Weil preparation. × 6.

Fig. 15 Transverse section through the diagonal band of Broca. Note fibers (y) of this system coming from the nucleus ansae peduncularis and the tuberculohabenular fibers (t). This series is somewhat tilted. Weil preparation. × 6.

Not all of the precommissural fornix fibers reach the septum by the above enumerated routes, for some fascicles of this system come forward with the main fornix bundles to enter the caudolateral part of the septum (fig. 18). In the septum the precommissural system is further augmented by fibers of septal origin and from other sources and it is not possible in all instances to distinguish between fibers of passage and fascicles in synaptic relationship with the septum.

Fibers from the lateral septal nucleus in their arching, descending course to the medial forebrain bundle, which is beginning at these planes to collect beneath the nucleus accumbens, pass anteriorly, posteriorly, and medially to the nucleus, thus encapsulating it. Also, both cross and sagittal Cajal silver series reveal fine, unmedullated fibers from the lateral septal nucleus which penetrate the capsule and enter the nucleus accumbens (fig. 16). However, not all of the fibers which descend in front of the nucleus accumbens are destined for the medial forebrain bundle, for immediately caudal to the level of figure 14, in all series studied, the large, well-known tuberculo-septal and septo-tubercular fascicles (von Kölliker, 1896; Elliot Smith, 1897), which extend into the polymorph layer of the tuberculum, are encountered. The greater percentage of fibers descending from the lateral septal nucleus to the medial forebrain bundle pass down the posterior side of the nucleus accumbens (fig. 18).

In the large-celled portion of the medial septal nucleus (fig. 16) there are deeply staining fibers which increase in number as this nucleus widens out posterior to the bulge of the nucleus accumbens. These fascicles—which represent a cephalic portion of the diagonal band—are a part of Zuckerkandl's (1888) 'Riechsbündel des Ammonshorns' and a part of the precommissural fasciculus of Elliot Smith (1897). Ramón y Cajal ('11) studied this fiber system in Golgi preparations of the mouse and considered it afferent with respect to the septum. As the level of the anterior commissure is approached, the cells of the medial septal nucleus are replaced by the nucleus of the diagonal band of Broca (fig. 13) and the fibers which

here form the main mass of the diagonal band accompany the latter nucleus in its sweep across the ventral part of the brain between the tuberculum olfactorium and the preoptic area. Passing ventral to the medial forebrain bundle (figs. 15, 18), the diagonal band gives off fascicles to this bundle and to the tuberculum olfactorium, and then, continuing its course to the lateral wall of the hemisphere, disperses in the anterior amygdaloid area; perhaps a few of its fibers reach the pyriform cortex. The correlation of the septal region and the anterior amygdaloid area by means of the diagonal band has been stressed by Johnston ('23), Loo ('31), Young ('36), and Humphrey ('36). It will be recalled that neurons from the nucleus of the diagonal band become continuous with a ventral extension of the globus pallidus. Fibers accompany these cells, and thus a connection is effected between the globus pallidus and the medial septal nucleus (fig. 15). Winkler and Potter ('14, plate IV) show this last described connection for the cat.

The supracommissural component of the stria terminalis enters the septal region immediately caudal to the posterior fibers from the lateral septal nucleus which are descending to the medial forebrain bundle (figs. 17, 18). This strial component sends some of its fascicles into the septum, providing a further correlation path between the septum and the amygdala. Moreover, as the supracommissural component of the stria terminalis swings over the anterior commissure to pass to preoptic and hypothalamic regions, precommissural fornix fibers are added to its medial side.

The connections of the nucleus septalis fimbrialis were given with the description of the nucleus (p. 31). It receives impulses from the descending columns of the fornix and its fibers relay these impulses through the stria medullaris to the habenula.

Crosby ('17) in her study of the forebrain of the alligator suggested the following differentiation between the medial and lateral septal nuclei, viz., "that the medial nucleus is a waystation for ascending impulses going towards the hippocampus, and the lateral nucleus is a similar station for descending

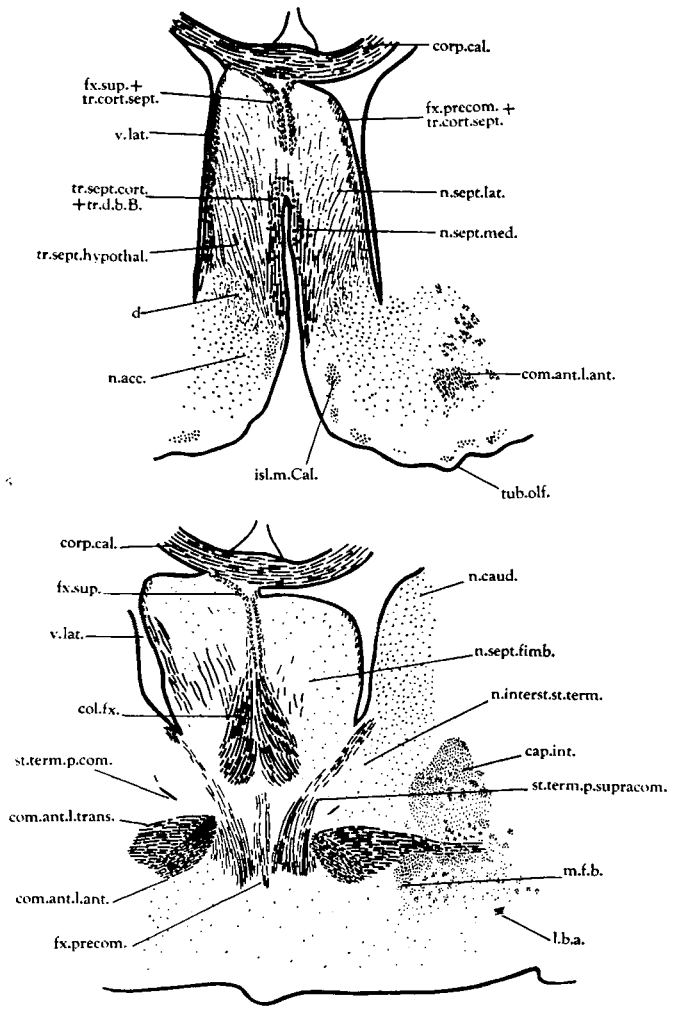


Fig. 16 Transverse section through the middle of the septum to show the fibers associated with the large-celled medial septal nucleus. Note the fibers impregnated in the ventricular part of the septum, and the fibers entering the nucleus accumbens. Cajal preparation. Three-week kitten. × 8.

Fig. 17 Transverse section through the caudal end of the septum to show the supracommissural component of the stria terminalis. Note the anterior division of the longitudinal association bundle. Cajal preparation. Three-week kitten. × 8.

impulses coming from the hippocampus." Loo ('31) and Young ('36) have followed this interpretation. Therefore, in the present account the fibers entering the lateral septal nucleus from the precommissural system are designated as cortico-septal and those leaving it to join the medial forebrain bundle are termed septo-hypothalamic. Similarly the precommissural fornix fibers related to the medial septal nucleus are

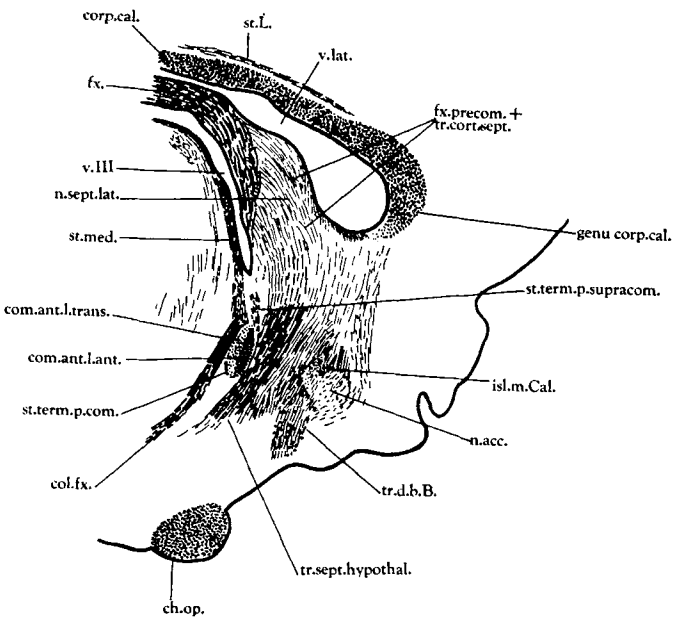


Fig. 18 Sagittal section through the lateral septal nucleus and the nucleus accumbens showing the precommissural fornix system and the relation of the tract of the diagonal band to the septo-hypothalamic tract. Cajal preparation. Three-week kitten. × 8.

designated as septo-cortical. However, the septal nuclei are more than way-stations in the path of the fornix fibers. The lateral septal nucleus, receiving impulses from the hippocampal and hypothalamic areas, projects these to the nucleus accumbens and to the caudate-putamen complex. The globus pallidus, which is efferent (Kodama, '29, and many others), discharges via its ventral extension and the associated gray

of the diagonal band back into the medial septal nucleus, providing then, within the septal region, for olfacto-somato-visceral correlations. Moreover, the diagonal band interconnects the septal area with the amygdaloid nucleus and the pyriform lobe areas, again making possible the correlation of olfacto-visceral with other modified types of olfactory impulses.

THE AMYGDALOID NUCLEI

The amygdala of the cat has been considered briefly by DeVries ('10), and part of this complex has been figured by Winkler and Potter ('14). One carnivore, Foetorius furo, is included in Völsch's ('10) detailed study of the amygdala in mammals. For the homologizing of the nuclei B, D, D′, E, M, T, and T′ of Völsch with Johnston's more recent and descriptive terminology see Johnston ('23) and Ariëns Kappers, Huber and Crosby ('36). Hilpert ('28) did not employ this terminology in his account of the amygdala in man.

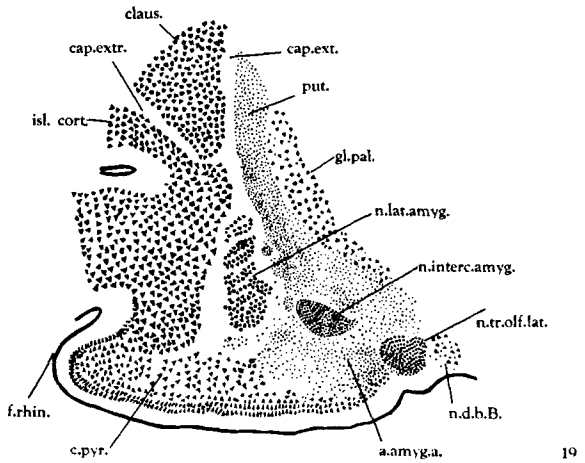
In the cat the amygdala occupies the medial part of the pyriform lobe and extends between the nucleus of the diagonal band of Broca anteriorly and the gray of the hippocampus posteriorly. Its position is discernible grossly, since two of its nuclei, the cortical nucleus outlined by the fissura amygdaloidea of Johnston ('23) and the nucleus of the lateral olfactory tract caudolateral to the tuberculum olfactorium, produce elevations on the ventral surface of the brain, which, as Loo ('31) pointed out in the opossum, correspond to the gyrus lunaris and the gyrus intermedius of Retzius respectively. The amygdaloid nuclei of the cat are essentially the same as those generally recognized in mammals since the work of Johnston ('23). In the present description it has been found convenient to consider them in three groups—lateral, medial, and anterior—on the basis of their position and fiber connections.

Lateral amygdaloid group

This group contains the lateral and basal nuclei and corresponds to the baso-lateral amygdaloid complex described by

Humphrey ('36) in the bat. Only a small portion of this division of the amygdala is related to the stria terminalis, the majority of its fiber connections being effected through the external capsule, the longitudinal association bundle, and the anterior commissure.

Lateral amygdaloid nucleus. The lateral amygdaloid nucleus, DeVries' ('10) corpus poststriatum, is the largest and longest nuclear mass in the amygdala. Due to its length and to the curve of the temporal pole of the hemisphere it appears concavo-convex in sagittal sections. It lies in the course of the external capsule, with which it is intimately associated and by which it is separated at all levels from the pyriform cortex. Posteriorly (fig. 24) it is the first of the amygdaloid nuclei to appear, and here the external capsule surrounds it on all sides except dorsally, in which region the lateral nucleus forms part of the floor of the lateral ventricle. In this ventricular position the lateral nucleus expands mediolaterally and meets the basal nucleus, which appears in the field (fig. 23). As the lateral nucleus increases, its dorsolateral angle, drawn out like the neck of a flask, extends farther dorsally into the external capsule (fig. 22) and comes into relationship with the tail of the caudate nucleus, which approaches the lateral nucleus but does not meet it. A few sections anteriorly, the ventricle closes and the tail of the caudate bends sharply to fuse with the putamen, which appears at the anterior end of the inferior tip of the lateral ventricle. At more anterior levels (fig. 21), in which all the nuclei of the amygdala are present, the lateral nucleus is bordered dorsally by the putamen and the central nucleus, medially by the basal nucleus, and ventrally and laterally by the external capsule, which separates it from the pyriform lobe cortex and the claustrum. This relationship persists rostrally as long as the basal and central nuclei remain in the field (fig. 20). The lateral nucleus, gradually decreasing on its medial side, extends forward into the external capsule, which surrounds it (fig. 19) on all sides. It has a striate appearance due to the fibers running through it to assemble in the anterior commissure. Johnston ('23) has called attention to the un-



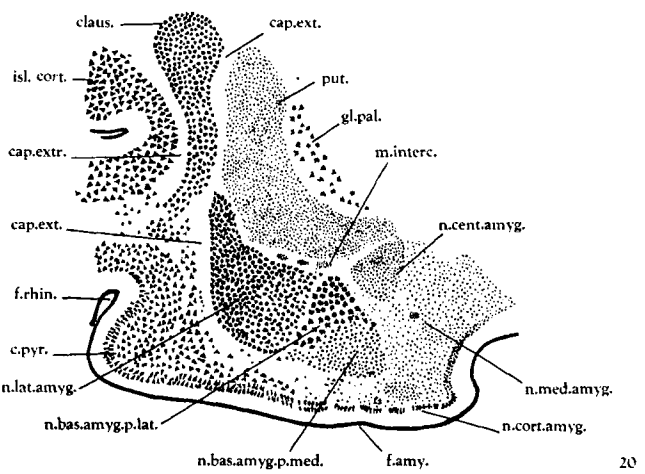


Fig. 19 Transverse section through the rostral end of the amygdala showing the nuclei in the anterior amygdaloid nuclear group. The lateral amygdaloid nucleus is completely surrounded by the external capsule. Toluidin blue preparation. × 6.

Fig. 20 Transverse section through the amygdala, caudal to figure 19, showing particularly the extension of the medial nucleus toward the lateral side of the preoptic area. Toluidin blue preparation. × 6.

usually great forward extension of this nucleus in Macacus rhesus, in which animal it lies beneath the anterior commissure nearly to the level of the caudal end of the tuberculum olfactorium. In the cat the cephalic tip of the lateral nucleus reaches the most caudal fibers of the transverse limb of the anterior commissure. The lateral nucleus cannot be divided into dorsal and ventral parts in the cat, as it can in the rat (Gurdjian, '28) and in Tamandua (Olive Smith, '30), nor does it show anterior and posterior parts as in the rabbit (Young, '36).

Basal amygdaloid nucleus. The basal nucleus does not extend so far rostrally or caudally as does the lateral nucleus, with which it is contiguous laterally except for the short distance in which the two nuclei are separated by the external capsule (fig. 24). Caudally it passes uninterruptedly into the transitional gray formed by the meeting of the hippocampal and pyriform cortices and the cortical amygdaloid nucleus (figs. 22, 23). During part of its extent, the basal nucleus assists in the formation of the floor of the lateral ventricle (fig. 22). Anterior to the closing of the ventricle it is in relationship dorsally with the central nucleus and medially with the medial nucleus (fig. 21). From the plane of figure 20 forward, the basal nucleus decreases progressively on its medial side and disappears at the level of the anterior amygdaloid area. Anteriorly and anteromedially its limits are rather definitely outlined by intercalated cell masses.

The basal nucleus has two distinct parts, a large-celled portion and a small-celled portion, as was noted by Völsch ('10) in Foetorius and since by various workers for different mammals. In the cat the cells of the large-celled portion are the deepest staining and largest cells in the amygdala, being slightly larger than the neurons of the lateral nucleus, whereas the cells of the small-celled portion of the basal nucleus are of medium size. The position of the large-celled portion of the basal nucleus is lateral to that of the small-celled portion. The disposition of these two divisions of the basal nucleus of the cat differs, then, from the relations found in the opossum

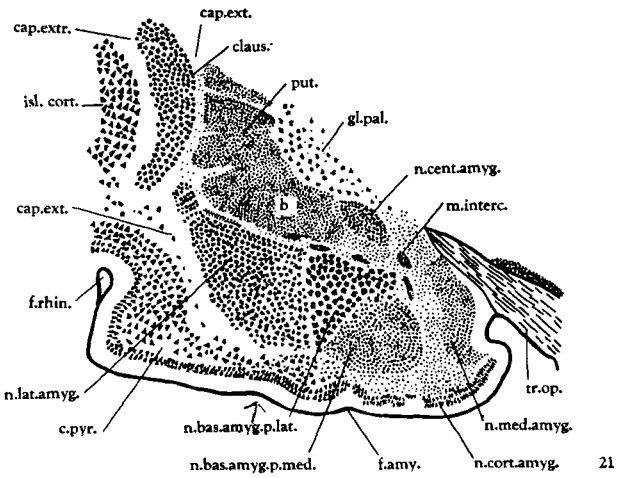
(Johnston, '23) and in Caenolestes (Obenchain, '25), in which the reverse position of these divisions of the basal nucleus prevails, but is similar to the condition found in Foetorius (Völsch, '10), Lemur (Völsch, '10), Macacus (Völsch, '10, and Johnston, '23), the rabbit (Young, '36), and the bat (Humphrey, '36).

Medial amygdaloid group

In this division are included the central, the medial, and the cortical nuclei—those amygdaloid nuclei particularly associated with the distribution of the stria terminalis. This group corresponds with the cortico-amygdaloid complex of Humphrey ('36), excepting that, in the present account, the nucleus of the lateral olfactory tract is included in the anterior group because of its rostral position.

Central amygdaloid nucleus. The central nucleus, the most dorsal of the amygdaloid nuclei (figs. 21 and 20), is ventromedial to the putamen and, in toluidin blue preparations, it is difficult to establish a boundary between these areas on account of the similarity of their neurons. In the opossum Johnston ('23, p. 412) separated them on the basis that the putamen, from which fascicles radiate through the globus pallidus and the internal capsule, is richer in myelinated fibers than the ventrally lying central nucleus. Using such a criterion, it is possible in the cat to assign, at certain levels, a considerable portion of the gray above the lateral nucleus to the central nucleus. This is particularly evident at such a level as figure 21b, but is less clear rostrally (fig. 20). There is, in the cat, a group of distinctly larger and deeper staining cells in that medial part of the central nucleus which lies immediately above the basal nucleus. This group is comparable in position to Völsch's nucleus E in Foetorius (see Völsch, '10, figs. 14, 15) and to the nucleus striae terminalis found by DeVries ('10) in the cat. If this differentiated portion be regarded as forming all of the central nucleus, then this nucleus is relatively small in the cat, is well developed only in the region in which the stria terminalis turns into the amygdala (fig. 21),

and has an anteroposterior extent less than that of the large mass of cells above the lateral nucleus. However, Völsch's nucleus E represents only a small part of the central nucleus later described by Johnston ('23). This more extensive area



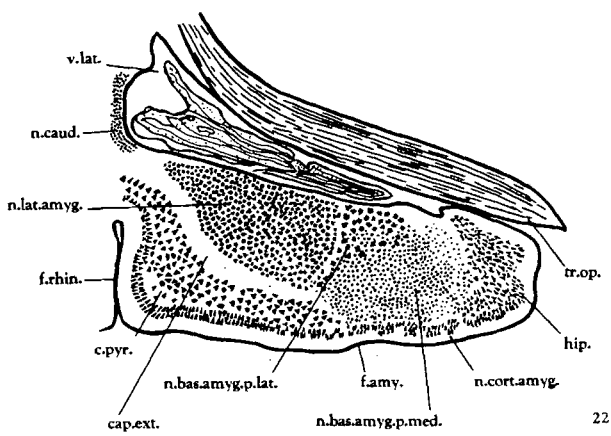


Fig. 21 Transverse section through the amygdala anterior to the inferior tip of the lateral ventricle, showing all the nuclei of the medial and lateral amygdaloid nuclear groups. Toluidin blue preparation. × 6.

Fig. 22 Transverse section through the amygdala, near the caudal end of the cortical amygdaloid nucleus. Toluidin blue preparation. × 6.

relegated by this last mentioned observer to the central nucleus is well outlined in the cat material by intercalated cell masses (fig. 21, m.interc.), which in the aggregate approach the Y-shape they present in the rabbit (Young, '36). The majority of the fibers of the stria terminalis descend on the medial side of the well-differentiated part of the central nucleus and, in their course, there are small cells which are continuous ventrally with the medial amygdaloid nucleus. They represent all that the cat possesses in the way of a strial bed in the temporal pole of the hemisphere.

The material studied seems to indicate that, in the cat, the central nucleus has two parts: a less extensive medial division and a larger lateral division. Furthermore, the larger lateral division, because of its resemblance to the putamen, might be designated as a putamen-central amygdaloid complex. The globus pallidus lies along the dorsal surface of both these divisions.

Medial amygdaloid nucleus. This is the largest and most medial nucleus of the medial amygdaloid group. It is wedged in the area between the central and the basal nuclei laterally and the optic tract and the preoptic region medially. Posteriorly it is narrow, where it borders the lateral side of the optic tract (fig. 21), but it widens out anteriorly as it faces the anterior side of this tract and extends to the lateral side of the preoptic region (fig. 20). Ventrally the medial nucleus descends to the cortical amygdaloid nucleus, and it approaches the small-celled portion of the basal nucleus laterally and the central nucleus dorsolaterally. It blends posteriorly with the gray of the hippocampus and anteriorly passes insensibly into the anterior amygdaloid area. Its cells are of medium size and are diffusely arranged, for this nucleus forms a bed for the distributing stria terminalis fibers and for other fiber systems of the amygdala.

Cortical amygdaloid nucleus (figs. 20, 21, 22). This nucleus is the most ventral member of the amygdaloid complex. It covers a circular area, outlined by the circular amygdaloid fissure, that is evident grossly on the surface of the brain. The

cells of the cortical nucleus are of the medium- and small-sized pyramidal variety and they make up a thin cortex-like layer, which, in places, is rather broken and corrugated in appearance and very suggestive of the pyramidal layer of the tuberculum olfactorium. This is particularly true at the posterior extremity of the cortical nucleus, in those levels in which it forms a cortical transition between the hippocampal and pyriform cortices. The cortical nucleus contacts the pyriform cortex laterally and is contiguous with the medial amygdaloid nucleus anteromedially and the hippocampal cortex posteromedially. Throughout its extent the small-celled portion of the basal nucleus lies directly dorsal to the cortical nucleus. With the disappearance of the basal nucleus rostrally, the cells of the anterior amygdaloid area cover the cortical nucleus dorsally and extend forward to form its cephalic border. At no place does the cortical nucleus become subcortical as it does in Erinaceus and Mus (Völsch, '06) and in the rabbit (Young, '36).

Anterior amygdaloid group

An anterior subdivision of the amygdala is made here for convenience of description, to which have been allocated the anterior amygdaloid area, the nucleus of the lateral olfactory tract, and the massa intercalata. The fiber connections of this group are effected through various channels, and one nucleus of this subdivision, the nucleus of the lateral olfactory tract, has connections through the stria terminalis. In the opossum (Johnston, '23, and Berkelbach van der Sprenkel, '26) and in the bat (Humphrey, '36), this latter nucleus was placed in the medial group on the basis of its connections with the stria terminalis and the lateral olfactory tract. In the present account it is included in the anterior group for topographical reasons.

Anterior amygdaloid area (fig. 19). At the anterior end of the amygdala, at levels in which the large-celled portion of the basal nucleus is no longer present and the anterior end of the lateral nucleus is well circumscribed by fibers of the ex-

ternal capsule, it is not possible to delimit the central nucleus, the medial nucleus, nor the small-celled portion of the basal nucleus. This is a transitional region and the contained cells, diffuse in arrangement, are continuous posteriorly with the better organized nuclei of the amygdala, medially with the nucleus of the diagonal band of Broca, laterally with the pyriform cortex, and anteriorly with the tuberculum olfactorium. Gurdjian ('28) employed the term 'anterior amygdaloid area' for this region in the rat.

Nucleus of the lateral olfactory tract (fig. 19). The nucleus of the lateral olfactory tract is a compact spherical mass of deeply staining neurons situated in the anteromedial part of the anterior amygdaloid area. Grossly it produces a rounded elevation on the surface of the brain. It overlies the medial edge of the lateral olfactory tract and is surrounded on its dorsal, lateral, posterior, and anterior surfaces by the cells of the anterior amygdaloid area. Its medial surface abuts the nucleus of the diagonal band of Broca. In the cat the nucleus of the lateral olfactory tract has not the subdivisions that have been reported for this nucleus in other forms, neither the dorsal and ventral parts found in Caenolestes (Obenchain, '25) and in the rat (Gurdjian, '28) nor the medial and lateral parts which occur in the rabbit (Young, '36) and in the bat (Humphrey, '36). However, for a short distance those cells of the anterior amygdaloid area which intervene between the pyriform cortex and the nucleus of the lateral olfactory tract are a trifle more compact than usual in this region and may represent a vestige of another subdivision of this nucleus.

The intercalated mass of the anterior amygdaloid area. The intercalated masses are condensed plates of small nerve cells compressed between certain of the amygdaloid nuclei. They were considered by Völsch ('10) as glial elements, but the consensus of opinion is now, following Johnston ('23), that they are true nerve cells. In the cat amygdala they occur caudally between the basal and central amygdaloid nuclei and then between the basal and medial amygdaloid nuclei in the path of the stria terminalis (fig. 21). Anteriorly they are

present above the lateral and basal nuclei in the course of the longitudinal association bundle and the fascicles closely associated with this system (fig. 20). As sections are followed anteriorly, the intercalated masses, above the lateral and basal nuclei, are like a string of beads (fig. 26). Near the cephalic

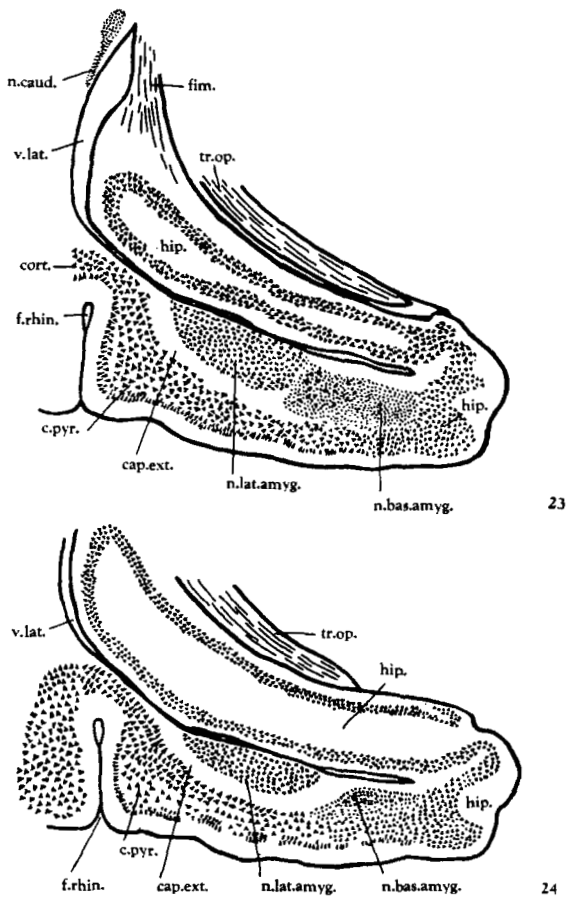


Fig. 23 Transverse section through the amygdala, at a level in which the lateral and the basal nuclei become contiguous. Toluidin blue preparation. × 6.

Fig. 24 Transverse section through the caudal end of the amygdala, showing the continuity of the basal nucleus with the hippocampus, and the separation of the basal nucleus from the lateral nucleus by the external capsule. Toluidin blue preparation. × 6.

end of the basal nucleus they enlarge until one of them, the most anterior, is worthy of special note. This rather large, oval, intercalated mass, which covers the anterior end of the basal nucleus and extends forward in the anterior amygdaloid area (fig. 19), lies at the midpoint of a straight line drawn transversely between the lateral nucleus and the nucleus of the lateral olfactory tract. Slightly greater in size than the nucleus of the lateral olfactory tract, it continues forward through the anterior amygdaloid area, beneath the transverse portion of the anterior limb of the anterior commissure, to become continuous with that part of the putamen cut off ventrally by the anterior commissure and termed, in the opossum (Loo, '31), the nucleus intermedius striati. This intercalated mass is the most rostral element of the amygdala. Gurdjian ('28) has described large intercalated masses in the rat and Humphrey ('36) found that in the bat similar intercalated masses enlarge caudalward in relation to the accessory basal nucleus.

Stria terminalis

The stria terminalis constitutes one of the principal pathways for certain of the amygdaloid nuclei, establishing connections for these nuclei with septal, preoptic, hypothalamic, and epithalamic centers. From the temporal pole to a level slightly caudad to the anterior commissure, the stria terminalis, arching around the internal capsule, passes as a compact bundle along the lateral ventricle in company with the tail and body of the caudate nucleus. In the posteroventral part of its course, as the stria rides over the optic tract and the lateral geniculate nucleus of the diencephalon (fig. 28), the tail of the caudate nucleus follows the lateral margin of the stria, which, convexly curved posteriorly, fits closely within the concave anterior surface of the fimbria-fornix complex. The stria loses this relationship with the fimbria and moves medialward to pursue the anterior part of its course. It then runs rostralward between the thalamus and the caudate nucleus to reach its bed nucleus just behind the anterior com-

missure. Throughout the course just described, the stria terminalis is in contact with the capsule fibers covering the superficial surface of the caudate nucleus (fig. 28, s.s.), which fibers von Kölliker (1896) called the stratum album superficiale (see also Poljak, '27, fig. 26, SSC). These capsule fibers continue over the head of the caudate, whereas the stria terminalis, in the vicinity of the anterior commissure, breaks up into the various portions designated by Johnston ('23) in the opossum as commissural, supracommissural, infracommissural hypothalamic, and stria medullaris components.

Certain difficulties are met with in analyzing the components of the stria terminalis. In the present material only one of these components is differentially stained and can be followed as an individual entity through the whole of its passage from the amygdala to the anterior commissure. It is impossible to trace the rest of the components as separate bundles after they are united in the stria terminalis. Furthermore, since the length of the stria terminalis is dependent upon the size and the development of structures (such as the internal capsule) over which it passes, it is longer in the cat than in most subprimates in which it has been well analyzed. In the present account the strial components will be considered first in the region of the anterior commissure, at which level these various bundles separate to pursue their several paths. The relations of the stria within the amygdala will be described later.

Relations of the stria terminalis in the anterior commissure region. Commissural component. This is a deep staining component in the ventrolateral part of the stria as this latter complex comes forward toward the anterior commissure. It leaves the other strial fibers at the bed nucleus and, descending in a ventrolateral loop (figs. 15, 17), bends sharply medialward to enter the postero-inferior part of the anterior commissure, in which region it stands out clearly in sagittal and cross sections (fig. 18) as a single bundle. In the rat (Gurdjian, '25) and in Tamandua (Olive Smith, '30) it is divided into two

bundles as it crosses in the commissure. In the cat all of the fibers appear to be truly commissural.

Supracommissural component (figs. 17, 18). This is the largest of the components and contains the majority of the stria terminalis fibers. It descends obliquely ventromedially through the strial bed and courses anterior to the anterior commissure, at which level it sends a few fascicles into the septal nuclei and to the posterior part of the nucleus accumbens. Ramón y Cajal ('11) illustrated in Golgi preparations of the mouse collaterals of this system which pass into the septum and, in the opossum (Johnston, '23; Loo, '31) and in the bat (Humphrey, '36), similar connections are said to be present. The supracommissural bundle flattens out on the anterior surface of the anterior commissure (fig. 17) and its fibers, together with those of its fellow of the opposite side, flank the precommissural fornix system and turn caudalward beneath the anterior commissure. In the Cajal cross section series of the 3-week-old kitten these fibers can be traced to the medial part of the preoptic region and to the anterior part of the hypothalamus (fig. 25).

Stria medullaris component (fig. 20). At the cephalic end of the anterior thalamic nucleus, the stria terminalis comes close to the stria medullaris and there is an exchange of fibers between these two systems. These fibers are few in number and difficult to follow as they pass from the medial side of the stria terminalis and weave their way through the fascicles of the thalamic radiations to join the stria medullaris. In the rabbit (Young, '36) and in the bat (Humphrey, '36) also, this component is small.

Preoptic component (fig. 29). The terminology of Gurdjian ('25) is followed in this account of the preoptic component since there are only a few fibers of the stria terminalis descending behind the anterior commissure. This component consists of thinly myelinated fibers which leave the ventral side of the stria terminalis and course in a diffuse manner through its bed nucleus. They are best seen in the sagittal series of the 3-week-old kitten, in which preparations they

can be traced to the preoptic region. It is impossible to determine in the present material whether or not any of them reach the hypothalamus. However, a few of the more lateral fibers run forward beneath the anterior commissure and perhaps are the equivalent of the infracommissural component of Johnston ('23). In the opossum (Johnston, '23 and Berkelbach van der Sprenkel, '26) there are two portions of the stria terminalis behind the anterior commissure, the infracommissural and the hypothalamic bundles. These hypothalamic bundles form the largest component of the stria terminalis in this form. Olive Smith ('30) described the same bundles in Tamandua. Gurdjian ('25) was unable to trace stria terminalis fibers of this system to the hypothalamus. Hence, the fibers behind the anterior commissure in the rat constitute a preoptic component. Young ('36) and Humphrey ('36) adopted this terminology and pointed out the homology between their preoptic component and the hypothalamic component of Johnston ('23). Apparently, in certain mammals, there is a reduction in the number of stria terminalis fibers proceeding to the hypothalamus by way of the hypothalamic bundle of Johnston ('23) and an increasing number of fibers are routed to this station via the supracommissural bundle.

Distribution of the stria terminalis in the amygdala. The stria terminalis, on entering the amygdala, is flattened like a ribbon along the lateral side of the optic tract (fig. 26). It gives off some fibers to the central nucleus as it curves first across the dorsocaudal edge and then around the dorsomedial side of this nucleus to reach a position above the small-celled portion of the medial nucleus (fig. 28). A few scattered fascicles are dispersed in the medial nucleus and, in the pyridine silver series of the 2-day-old kitten, fine, unmedullated fibers can be traced through the medial nucleus and the small-celled basal nucleus to the cortical amygdaloid nucleus. However, the major portion of the stria terminalis, on reaching the dorsomedial surface of the small-celled basal nucleus, turns caudoventrally and distributes to the caudal part of both divisions of the basal nucleus (fig. 27).

The commissural component is in the dorsolateral segment of the stria as it descends into the amygdala, after which it separates from the rest of the stria (fig. 26) to swing across the dorsocaudal part of the central nucleus and, on gaining the dorsolateral edge of the medial nucleus, turns rostrally (fig. 25). It then runs anteroventrally through the medial nucleus (fig. 27) and breaks up into small fibers on the posterior surface of the nucleus of the lateral olfactory tract.

In analyzing the distribution of the various components of the stria terminalis in the amygdala, the commissural component alone is clearly defined and presents no difficulty. Within the supracommissural component there are probably some fibers from the posterior and medial portions of the basal nucleus since in the anterior commissure region the supracommissural component takes in the majority of the stria terminalis, although in the amygdala the greatest percentage of the stria fibers distribute to the posterior and medial parts of the basal nucleus.

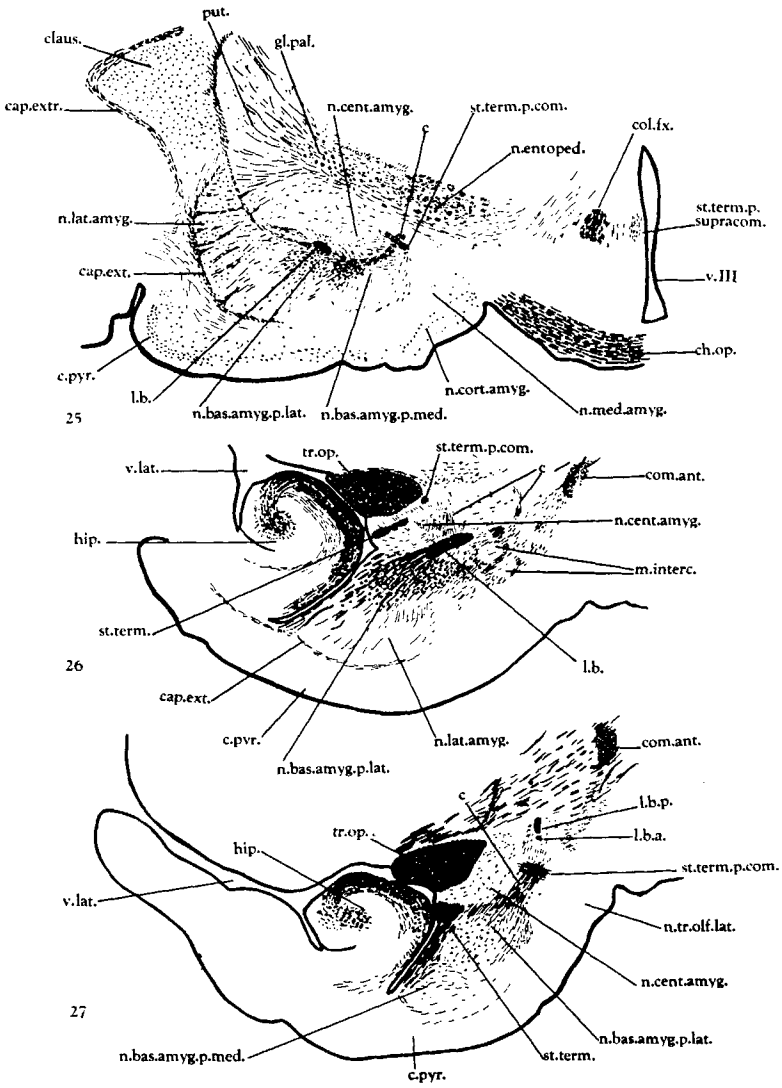
The longitudinal association bundle

This bundle begins to form at the level at which the stria terminalis dips into the amygdala (fig. 28, l.b.). A short distance anteriorly it appears as a large, oval bundle below the central nucleus and dorsal to the point of meeting of the basal and lateral nuclei (fig. 25, l.b.). It is the amygdalo-pyriform association bundle of Johnston ('23). Earlier workers applied

Fig. 25 Transverse section through the middle of the amygdala showing the formation of the longitudinal association bundle. Note the diffuse fibers (c) which cut across the commissural component of the stria terminalis. Cajal preparation. Three-week kitten. × 8.

Fig. 26 Sagittal section through the amygdala to show the formation of the longitudinal bundle and the separation of the commissural component from the rest of the stria terminalis. Note the massa intercalata anterior to the basal nucleus. Cajal preparation. Three-week kitten. × 8.

Fig. 27 Sagittal section of the amygdala medial to figure 26. The longitudinal bundle is seen splitting into two divisions. The commissural component of the stria terminalis extends to the nucleus of the lateral olfactory tract and the remainder of the stria distributes to the caudomedial part of the basal nucleus. Cajal preparation. Kitten, 3 weeks. × 8.



Figures 25 to 27

the name 'sagittales Längsbündel' to this fasciculus, and Völsch and others employed the same term in describing the commissural component of the stria terminalis. The manner of formation of the longitudinal association bundle is clearly revealed in the Cajal sagittal series of the 3-week-old kitten, in

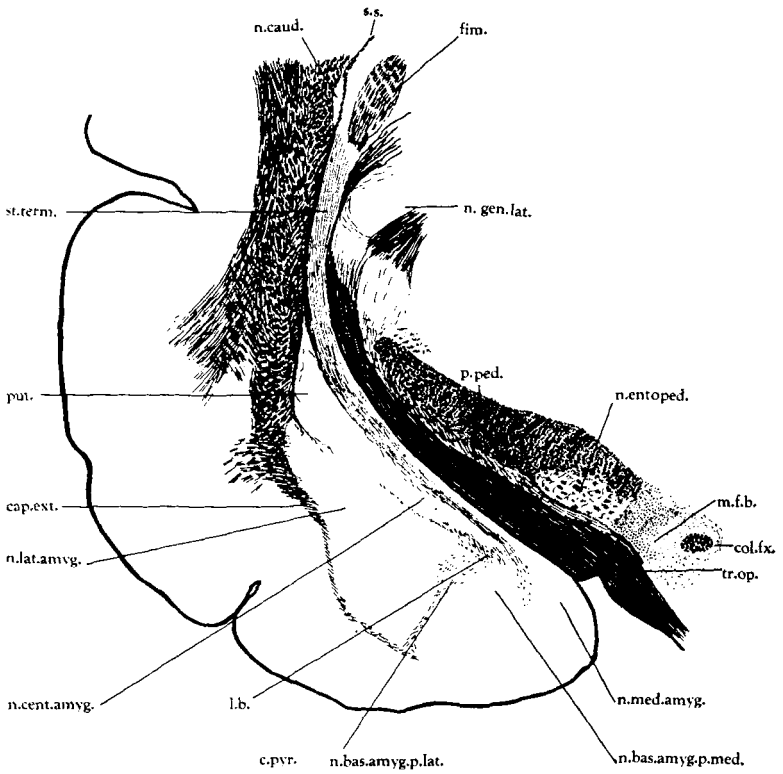


Fig. 28 Transverse section showing the relations of the stria terminalis as it descends to the amygdala. The longitudinal association bundle is beginning to form. Weil preparation. × 6.

which it is especially well impregnated. Fibers enter the lateral nucleus posteriorly and laterally from the pyriform cortex. Some of them end in the lateral nucleus. Others, joined by fascicles from this nucleus, proceed in a diagonal direction dorsally, medially, and rostrally to enter the longitudinal association bundle (fig. 26, l.b.). This bundle is further

increased by the addition of fibers from the anterior one-half of the basal nucleus, over which it lies as it continues forward. Near the anterior end of the basal nucleus this bundle curves dorsomedialward through the central and medial nuclei, spliting up in the latter nucleus (fig. 27) into a larger posterior bundle (l.b.p.) and a smaller anterior bundle (l.b.a.). The posterior bundle, which continues medialward beneath the internal capsule, can be traced as far as the preoptic area. The smaller anterior bundle descends rostroventrally through the anterior amygdaloid area, in which area it turns medialward, and, passing beneath the anterior commissure (fig. 17, l.b.a.), joins the lateral side of the medial forebrain bundle. Once incorporated within this latter formation, its destination is difficult to determine. It may extend as far caudad as the hypothalamus.

The longitudinal association bundle, projecting impulses from the pyriform cortex and the amygdala, is comparable, in part at least, to the ventral olfactory projection tract described in the alligator (Crosby, '17) and in the opossum (Loo, '31), and to the lateral cortico-hypothalamic tract identified in the rat (Gurdjian, '27) and in the armadillo (Howe, '33).

External capsule and anterior commissure connections of the amygdala (fig. 29)

The lateral amygdaloid nucleus is intimately associated with the external capsule and, at its posterior end, is in receipt of cortico-amygdaloid connections from other than pyriform cortex by way of the external capsule. Further, the lateral nucleus not only receives fibers from the pyriform cortex by this same route, but also sends fibers into the external capsule which then make their way into the posterior limb of the anterior commissure. This is particularly evident at the anterior end of the lateral nucleus, in which region these two kinds of fibers are more easily followed. Here the obliquely passing fibers from the pyriform cortex cut the lateral nucleus into segments. Such fibers are cross hatched by finer, more vertically and dorsally running fibers originating within the

lateral nucleus which enter the posterior limb of the anterior commissure. The anterior end of the large-celled portion of the basal nucleus likewise sends fibers into the posterior limb of the anterior commissure. This is best seen in the sagittal series, in which the large intercalated mass that caps the anterior end of the basal nucleus is encapsulated by thinly myelinated fibers streaming from the surface of the basal nucleus and from the intercalated mass and entering that part of the anterior commissure. Such fibers pass directly over the large intercalated mass of the anterior amygdaloid area. In the bat, Humphrey ('36) followed fibers from the lateral and basal amygdaloid nuclei into the anterior commissure and was able, in midsagittal sections, to distinguish these respective amygdaloid components from the other components of the commissure.

Other amygdaloid connections

The silver preparations show that the amygdala is loaded with a surprising number of diffuse fibers which cannot be allocated to either the stria terminalis or the longitudinal association bundle. These fibers radiate through the basal and lateral nuclei and cut around and through the longitudinal bundle. At one point they form a rather strong fasciculus, which receives additional fibers from the central nucleus and crosses the commissural component of the stria terminalis at right angles (figs. 25, 27, c). This bundle can be followed as far as the nucleus entopeduncularis, in which region it disappears. A little anterior to the level of figure 25, similar diffuse fascicles can be traced across the lateral, basal, and medial nuclei to the lateral part of the preoptic area. In the anterior amygdaloid area such fibers are extremely numerous, and in their lateromedial passage to the preoptic area they outline the large intercalated mass.

Summary of the amygdaloid connections (fig. 29)

The amygdaloid connections are here summarized in a diagram showing four characteristic levels of the amygdala. On

the right side of the figure the stria terminalis is shown and on the left side the longitudinal association bundle and the posterior limb of the anterior commissure. In the midline are representations of the anterior commissural level and the preoptic, the hypothalamic, and the epithalamic regions. The

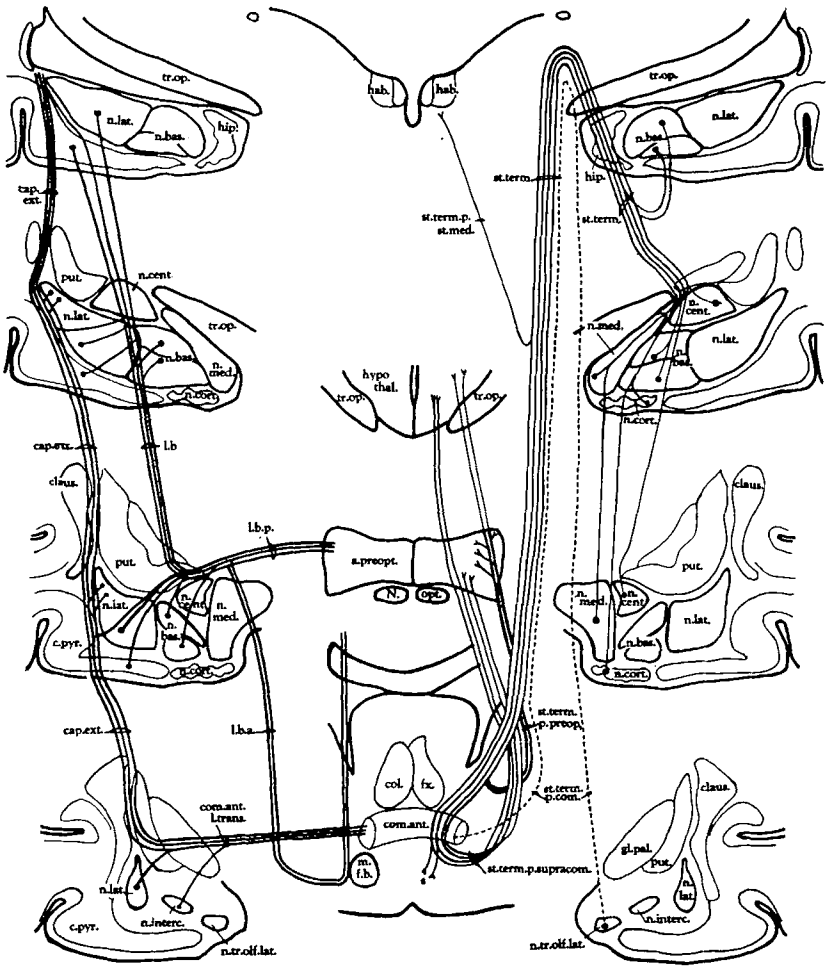


Fig. 29 Diagram of some of the fiber connections of the amygdaloid complex. On the right side of the figure is the stria terminalis. On the left side are the external capsule, the transverse limb of the anterior commissure, and the longitudinal association bundle. In this figure the abbreviation 'amyg.' is omitted from the labels for the various amygdaloid nuclei, because of lack of space.

stria terminalis connects with the cortical, the medial, the central, and the posterior and medial parts of the basal amygdaloid nuclei. The one well-defined component of the stria terminalis system is a commissural component, which interconnects the nuclei of the lateral olfactory tract. Connections between the amygdala and the habenula, though present, are extremely small, as is evidenced by the minute size of the stria medullaris component of the stria terminalis.

The lateral nucleus and the anterior and lateral parts of the basal nucleus have nearly identical connections. Both are connected with the preoptic area and perhaps also with the hypothalamus by way of the longitudinal association bundle and each is interconnected with its fellow of the opposite side by way of the anterior commissure. However, the lateral nucleus receives cortico-amygdaloid fibers from the pyriform cortex and bundles from an unknown source through the external capsule. Not shown in the diagram are the diffuse fibers which connect the various amygdaloid nuclei with the preoptic region and the diagonal band fibers which correlate the anterior amygdaloid area with the septal area.

GENERAL DISCUSSION

The primary, secondary, and tertiary olfactory centers of the cat are well developed. The olfactory bulbs and the associated accessory olfactory bulbs are of good size. The gray of the olfactory crus, the anterior olfactory nucleus, exhibits a rostrocaudal differentiation and merges posteriorly with the pyriform and frontal cortices, the tuberculum olfactorium, and the anterior continuation of the hippocampus.

The tuberculum olfactorium is a highly specialized structure containing large granule cell islands of Calleja, which are best developed in the more medial portion of the tuberculum. The most medial of these islands is the largest of all and is closely associated with the lateral septal nucleus and with the nucleus accumbens. The tuberculum sends a number of fibers to the stria medullaris; presumably they go to the habenula. The septum provides an area of passage for the

precommissural fibers of the fornix and serves as a relay station for impulses passing in both directions between the hypothalamus and the hippocampus. Also it is well provided with fiber connections to and from the tuberculum olfactorium. The nuclear masses of the septum have been divided into two lines of gray, a medial and a lateral, in order to emphasize the relationship existing between this ventromedial quadrant of the hemisphere and the basal and striatal portions of the lateral hemisphere wall. The diagonal band formation establishes a cellular and a fibrous continuity between the medial septal nucleus and the anterior amygdaloid area and between the medial septal nucleus and the anteroventral extension of the globus pallidus. Fibers from the lateral septal nucleus end in the nucleus accumbens. Herewith, then, is provided the necessary mechanism for the exchange of impulses between the septum and the striatum. Moreover, it seems logical to assume, from the work of Kodama ('29) and many others, that the globus pallidus, being efferent, sends impulses into the septum, whereas the cells of the lateral septal nucleus have descending neuraxes (based on Golgi studies available in the literature) and must then discharge their impulses into the accumbens-caudate complex. Thus the septum is an olfacto-somato-visceral correlation center.

The amygdala has been divided into three nuclear groups—medial, lateral, and anterior—each of which has characteristic connections. The importance of the various fiber systems outside of the stria terminalis—such as the external capsule, the anterior commissure, the very rich system of direct and diffuse fibers to the preoptic area, and, above all, the longitudinal association bundle—has been stressed. The distributions of the stria terminalis and of the longitudinal association bundle within the basal nucleus are of particular interest since within this nucleus occurs a somewhat indistinct line of separation between these two systems. Further, it has been shown that the lateral amygdaloid nucleus receives cortico-amygdaloid fibers. Of interest to experimenters is the fact that two of the

amygdaloid nuclei, the cortical nucleus and the nucleus of the lateral olfactory tract, form eminences on the brain surface. Once the location of these nuclei is established the position of the other amygdaloid nuclei can readily be determined.

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